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Coordinate Changes in Assimilatory Sulfate Reduction are Correlated to Salt Tolerance: Involvement of Phytohormones

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Authors' contributions

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Review Article

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ABSTRACT

Salt stress affected areas are increasing significantly all over the world leading to the adverse effects on plant growth and development and productivity of agricultural crops. For better suitability of plants with the changing environment, plants show well-defined metabolic alterations primarily in response to nutrient availability in the environment as an adaptive response. Thus, the management of salt stress is a function of nutritional status of the plant. The uptake and assimilation of sulfur plays a pivotal role in development and metabolic processes of plants and is an integral part of several important compounds, such as vitamins, co-enzymes, phytohormones and reduced sulfur compounds that decipher growth and vigour of plants under optimal and stressful environments. Assimilatory sulfate reduction may induce salt tolerance by coordinating various physiological processes and molecular mechanisms which are likely to be induced by phytohormones. The present review provides an update on physiological and molecular approaches associated with salt stress and details out how sulfur assimilation and phytohormones induce salt tolerance.

Keywords: Salt stress; sulfur assimilation; phytohormones; glutathione.

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CONTENTS

1. INTRODUCTION

Plants adopt several strategies against the changing environmental conditions such as temperature, light, minerals, water and other abiotic and biotic factors for their survival. Salt stress is one of the oldest and major global abiotic stresses that limit growth and productivity of crop plants. More than 800 million hectares of land all over the world, nearly about 6% of the world's total land area is salt affected [1]. It has been estimated that about 50% of the arable land will be affected by salt stress by the year 2050 [2]. The increasing land area by salinity urges the need to develop strategies to enhance crop production under saline conditions. It is, therefore, necessary to understand physiological processes and molecular mechanisms that plants operate to develop salt resistance for sustainable crop production. High levels of sodium (Na^+) and chloride (Cl^-) contents are accumulated in plants growing under salt stress, which disturb the homeostasis of essential nutrients, and plants tend to maintain desirable K^+/Na^+ ratio in cytosol to adjust with salt stress [3,4]. Moreover, an unavoidable consequence of high accumulation of Na^+ and Cl^- in plants is the excess production of reactive oxygen species (ROS) that impedes the physiological process. In a study on mungbean grown under salt stress, it has been found that excess accumulation of leaf Na^+ and Cl^- results in ROS production and reduced photosynthesis and plant growth [5]. The overproduction of ROS also causes damage to DNA such as base deletion, pyrimidine dimers, cross-links, strand breaks, base modification and activation of programmed cell death [6,7]. Thus, to prevent ROS from damaging cellular components, plants tend to develop multiple detoxification mechanisms [8].

Mineral nutrients have shown promising potential in alleviation of salt stress [9,10]. Sulfur (S) is the fourth major essential nutrient element after nitrogen (N), phosphorus (P) and potassium (K) that plays an important role in stress tolerance in plants [11,12]. It also plays an important role in improving K^+/Na^+ selectivity to increase the capability of calcium ions (Ca^{+2}) and to decrease the induced injurious effects of Na^+ ions [5]. Sulfur-containing compounds have shown increased tolerance to salt-stressed plants by modulating physiological processes and by up-regulating specific genes for stress tolerance [13]. Kim et al. [14] have reported that *O*-acetyl serine (OAS) regulates the incorporation of S and N into cysteine (Cys) and the synthesis of reduced glutathione (GSH) to maintain reduced state of the cell. GSH plays essential roles within plant metabolism and stress tolerance to ROS [15].

Phytohormones interact with nutrients synergistically or antagonistically and regulate plant growth and development under optimal and stressful environments. Phytohormones such as cytokinins; CK [16], auxins [17], gibberellins; GA [18], ethylene [19], nitric oxide; NO [20], jasmonates; JA [21] and salicylic acid; SA [22] play essential roles in alleviating salt stress by regulating plant growth and development. For example, methyl jasmonates are involved in the mechanisms of tolerance of *Pisum sativum* [23], GAs induce salt tolerance in *Oryza sativa* as revealed by proteomics [24] and SA alleviates salt stress by inducing enzymes of S and N assimilation [5]. The roles of glutathione and GSH/thiol disulphide status in signal transduction cascade and modulation of phytohormones signaling pathways have been shown [25]. It shows that the interaction of phytohormones and S assimilation is crucial in stress tolerance. It is, therefore, important to identify and scrutinize how much S assimilation is induced by phytohormones to counteract the deleterious effects of salt stress. The understanding of the role of phytohormones in the regulation of S assimilation will give more insight into the S assimilation-induced salt tolerance. The present review provides a comprehensive account of the studies carried out in the area of regulation of salt tolerance through S nutrition employing physiological mechanisms and molecular tools with special emphasis on the involvement of phytohormones.

2. AN OVERVIEW ON PLANTS RESPONSES TO SALT STRESS

The effects of salt stress on plants are complex and its adverse effects include nutrient imbalance and deficiencies, ion toxicity and water deficits. One of the biochemical changes occurring in plants subjected to salt stress is the accumulation of ROS. It includes free radicals such as superoxide anion (O_2^-), hydroxyl radical ($OH^\bullet$), as well as non radical molecules like hydrogen peroxide (H_2O_2), singlet oxygen ($:O_2$) by the impairment of the cellular electron transport within different sub cellular compartments such as chloroplasts and mitochondria. In chloroplasts, various forms of ROS are generated and induce stomatal closure which leads to reduced CO_2 availability and inhibits carbon fixation. In addition, salt stress-induced necrotic areas in leaves have oxidative metabolism due to disturbed equilibrium between the production and the scavenging of ROS [26].

Salt stress activates the mitogen-activated protein kinase (MAPK) pathway that reduces stress associated ROS levels and increases tolerance to salt stress [27,28]. It has been reported that salt stress activates the expression of *AtMPK3, AtMPK4* and *AtMPK6* in Arabidopsis [29] and *MAPKs, ZmMPK3, ZmMAPK5* and *ZmSIMK1* in *Zea mays* [30, 8]. Salt tolerance and the intracellular Na^+ homeostasis are modulated through Ca^{2+} by the calcineurin B-like protein (CBL), CBL4/SOS3 (salt overly sensitive 3) and its interacting protein kinase CIPK24/SOS2 [31]. CBL4 encoded by SOS3 presumably senses the salt-elicited calcium signal and translates it to downstream responses. SOS3 interacts and activates SOS2, a serine/ threonine protein kinase. Active SOS2 kinase could also enhance a Na^+/ H^+ exchange activity in purified plasma membrane vesicles and salt stress allows the phosphorylation and activation of the membrane bound Na^+/H^+ antiporter, SOS1 [31]. Its activity may also be regulated by SOS4, which catalyzes the formation of pyridoxal-5-phosphate, a cofactor that may serve as a legend for SOS1. SOS2 is found to interact with nucleoside triphosphate kinase 2 (NDPK2) involved in ROS signaling [32]. In addition, Versules et al. [32] have shown that deficiency in *AtNDPK2* increases the salt sensitivity of Arabidopsis and also enhances the sensitivity of SOS2 mutants to salt stress. Therefore, the SOS pathway is critical for salt-stress tolerance in Arabidopsis, and plays a key role in regulating ion transport under salt stress [33].

Plants possess a complex antioxidative defense system comprising of nonenzymatic and enzymatic components to scavenge ROS. GSH, ascorbate (AsA), carotenoids, and tocopherols are non-enzymatic antioxidants. Enzymatic defense components include peroxidase (POD), superoxide dismutase (SOD) and catalase (CAT), which together with the other enzymes of the ascorbate–glutathione cycle such as ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and glutathione reductase (GR) promote the scavenging of ROS [34]. Among the non-enzymatic antioxidants, GSH is involved in ROS scavenging and maintaining steady-state ROS level. The increase in the GSH redox state is a better antioxidative protection and considered as an acclimation response to salt stress [35]. The reduction in AsA redox state associated with increase in GSH redox state represents an efficient interactive mechanism between enzymatic and non-enzymatic protection to avoid oxidative damage under high salt stress [36]. Enhanced expression and/or activity of antioxidative enzymes with the regulation of gene expression have also been associated with salt tolerance [37]. Differential genomic and proteomic screenings carried out in *Physcomitrella patens* plants showed that they responded to salt stress by up-regulating a large number of genes involved in antioxidant defense mechanism [38]. Sharma et al. [6] suggested that a higher status of antioxidants (AsA and GSH) and a coordinated higher activity of the enzymes (SOD, CAT, GPX, APX, and GR) could serve as the major determinants in the model for depicting salt tolerance.

3. UPDATES ON PHYSIOLOGICAL AND MOLECULAR APPROACHES ON SALT TOLERANCE

The increasing knowledge of genomics in the recent era has helped in the understanding of the mechanism and augmentation of salt stress [39,40,41]. Molecular markers offer specific advantages in assessment of genetic diversity and in trait-specific crop improvement which control salt stress by bulk segregate analysis (BSA). Moreover, molecular markers are also associated with genes or quantitative trait loci (QTLs) to improve salt tolerance via marker-assisted selection (MAS) in different crop species and acquiescent towards manipulation with current molecular genetic techniques [42]. The genome expression analysis can be conducted via cDNA-AFLP, an AFLP-based transcript profiling method used to identify differentially expressed genes in any species without the need for prior sequence knowledge. This method has been found of widespread use in temporal quantitative gene expression analysis and in gene discovery studies due to its fragment detection ability [43]. Using cDNA-AFLP technology, differentially expressed genes are analyzed between the salt-tolerant and the salt-sensitive under salt stress [44]. Recently, cDNA amplified fragment length polymorphism (cDNA-AFLP) has been used to detect differential gene expression in leaves of *Chrysanthemum lavandulifolium* in response to salt stress [44]. Several studies have shown that wild ancestors of cultivated plants such as *Spartina alterniflora* by Baisakh et al. [45] and *Gossypium hirsutum* by Rodriguez-Uribe et al. [46] are the major genetic resources of plant tolerance to salt stress. In fact, *Asteraceae* family species have unique mechanisms i.e., diploid genome that enable them to survive in salty and dry conditions. These mechanisms can help in finding useful gene resources to improve the ability of cultivated plants to grow under salt stress conditions. Stress tolerance can be increased by over-expressing ROS responsive regulatory genes that regulate a large set of genes involved in acclimation mechanisms. Plant transcriptome analysis measures gene expression differences under different abiotic stresses such as drought, cold and salt in a high-throughput manner [47]. Overexpression of the wheat salt tolerance-related gene *TaSC* enhances salt tolerance in Arabidopsis [40]. Similarly, overexpression of the mitochondrial *PPR40* improves salt tolerance in Arabidopsis by weakening the generation of ROS by stabilizing the mitochondrial electron transport and protecting Arabidopsis via reducing oxidative damage during salt stress [48]. *PeSP1* is a dodecamer homo oligomeric protein of around 148 kDa highly expressed in the *Populus eupharitica* plant which shares the biophysical properties with *SP1* and its expression is upregulated on NaCl stress and assists in the improvement of salt tolerance [49]. Similarly, Tuteja et al. [50] isolated 34 salinity tolerant genes and reported that pea lectin receptor like kinase and their homology resembled with lectin receptor like kinase (*LecRLK*) expression and was up-regulated on the response of salt stress resulting in salt tolerance. In addition to this, the transgenic approach allows the incorporation of only the specific cloned genes into an organism and restricts the transfer of undesirable genes from the donor organism. The dehydration-responsive element binding (DREB) transcription factors, which specifically interact with dehydration-responsive element (DRE)/c-repeat sequence (CRT) (A/GCCGAC), play an important role in plant environmental stress tolerance by controlling the expression of many stress related genes, such as *kin1*(protein serine-threonine kinases 1) anderd10 (early responsive to dehydration 10). DREBs contain a conserved apetala2/ethylene response factor (AP2/ERF) domain of approximately 60 amino acids [51].

4. SULFUR ASSIMILATION AND SALT TOLERANCE

Mineral nutrients are an important and integral part of the agricultural system. The presence of saline environment adds a new level of complexity to the mineral nutrition and sustainability of crops. Under saline environment, changes in root tissue make it more difficult for water and nutrients to move through the root membrane [52] and also deteriorate the efficiency of shoot [53]. Reports on the interaction of salt stress with mineral nutrients for salt tolerance are available [9]. Saeid et al. [54] reported that phosphorus ameliorated the adverse effects of water deficit, regulated the osmotic potential and maintained the osmotic stress in cucumber. Similarly, adequate supply of S has been shown to influence the growth and photosynthetic functions to a great extent and protect the barley crops from the adverse effects of salt stress [55]. Anjum et al. [56] have observed that N and S supply played an important role in plant growth, development and productivity in *Olieferous brassicas* cultivars through S-N mediated synthesis of plant antioxidant defense compounds.

4.1 Sulfur in Plants

Sulfur has a variety of vital functions within the plant. Inorganic S is converted to S-containing compounds as Cys and methionine (Met) and to secondary products such as sulfoxides and glucosinolates through a cascade of enzymatic steps [57]. S compounds hold essential functions in plant primary metabolism as structural components of proteins, lipids through the formation of sulfhydryl (S-H) and disulfide bonds (S-S), thioredoxin as regulatory molecules, metal-binding molecules, and as cofactors/ coenzymes such as CoA and S-adenosylmethionine (SAM), sulfolipids; vitamins i.e. biotin and thiamine; and peptides for biochemical reactions.

Over recent years, S deficiency is becoming widespread in many regions of the world. Occurrence of S deficiency has been described in cereals as well as in other crops mainly because of strong decrease in the inputs of S from atmospheric deposition and the use of low-S fertilizers. It might also be due to the intensive agriculture and optimization during plant breeding programmes that has resulted in the increased removal of S nutrients from soils thereby causing yield loss of agricultural crops [58].

4.2 Regulation of Sulfur Assimilation

S assimilation is highly regulated in a demand-driven manner [59,60,61] and is available to plants predominantly in the oxidized form of inorganic sulfate in the soil solution. Sulfate is taken up into plant cells via sulfate transporters; *SULTR 1; 2* (sulfate-H^+ co-transporters M) driven by the proton motive force created by ATPase [62]. Sulfate withdrawal from the growing medium decreases the levels of Cys, and GSH in canola plant tissues leading to the induction of *SULTR1; 2* systems and key enzymes along the assimilatory pathway [59].The key regulatory steps of sulfate assimilation are the activation of sulfate into the cells by ATP-sulfurylase (ATPS) and the reduction of adenosine 5-phosphosulfate (APS) to sulfite by APR [63]. There are two ATP sulfurylase isoforms in most plants: a major form localized in plastids and a minor form localized in the cytoplasm. It has been shown that when cultured tobacco cells and cultivar of rapeseed are exogenously supplied with S in the form of sulfate, the activity of APR and ATPS quickly returns to the normal levels [59]. OAS accumulates during S starvation and may thus serve as a signal of the S status [64]. In the chloroplasts, APS is reduced by APR (also APS sulfotransferase) to sulfite and further reduced to sulfide and incorporated into Cys by coupling to OAS and controlled by the enzyme OAS thiol lyase, also called cysteine synthase. The OAS needed for this reaction is produced by serine acetyltransferase (SAT). OAS acts most probably as a transcriptional regulator since its addition strongly increases mRNA levels of all the three APR isoforms and also those of sulfite reductase (SiR), chloroplastic *O*-acetyl-serine (thiol) lyase (OASTL), and cytosolic SAT [65]. Cys can be transferred to Met, incorporated into proteins or converted to SAM via reaction with ATP by SAM synthetase. Cys and Met are the two primary S products that require interactions with both N and C metabolism. Cys is the immediate metabolite for the production of GSH. The coordinated functions of S, N and C are likely to strengthen the salt stress tolerance and are able to assist S assimilatory reduction pathway for regulation of salt stress in plants.

4.3 Sulfur in Salt Tolerance

Sulfur plays essential roles in salt tolerance via synthesis of S-containing compounds. The S-containing group called thiol is strongly nucleophilic, preferably suitable for biological redox reactions and plays an important role in protection against salt stress-induced oxidative damage [9]. Tri-peptide GSH facilitates redox homeostasis in the cell [15] and is an abundant compound in plant tissue that exists interchangeably with the oxidized form, GSSG. GSH has been found associated with cell differentiation, cell death and senescence, pathogen resistance and enzymatic regulation in Arabidopsis [25], and its content is affected by S nutrition [66]. Adequate S supply may improve the pools of GSH in mustard to a great extent which may lead to increase in photosynthetic efficiency and subsequently to plant dry mass and yield [57]. Salt tolerance in plants has been associated with their capability to synthesize GSH and indicates a potential role of the S nutrition [9]. Salt stress increases the activities of SAT and OASTL leading to higher rate of Cys biosynthesis, which results in increased accumulation of GSH for defense responses to salt stress [13,67]. Ruiz and Blumwald [67] reported that S assimilation rate and biosynthesis of Cys and GSH were greatly increased in *Brassica napus* plant exposed to saline conditions. Furthermore, changes in S assimilation enzymes have been reported due to salt stress in Arabidopsis and broccoli [68, 69] respectively. Astolfi et al. [55] reported that salt-stress affected root thiol content by affecting the rate of S assimilation. Transgenic approaches have been used successfully to enhance the capacity of salt tolerance in plants through manipulating S metabolism. Overexpression of sulfate transporters, ATP-sulfurylase, Cys, OAS and GSH resulted in increased resistance to oxidative stress [70]. The control of S partitioning and manipulating the synthesis of S-containing compounds in plants using genetic engineering may be a potential option for increasing salt tolerance [71].

In plants, S- containing compounds such as Met, thioredoxins, vitamins (biotin and thiamine), CoA also play an important role in salt stress responses in addition to Cys and GSH [13]. These compounds have potential to modulate physiological processes of plants to enhance the salt tolerance competence. Met acts as a regulatory molecule as a part of SAM. The level of SAM synthase (an enzyme in SAM synthesis from Met) increases significantly under salt stress, suggesting the sensitivity of Met pathway to salt stress and its supplementation has been reported to increase salt tolerance [72]. Thioredoxins are small (12-13 kDa) heat-stable, ubiquitous protein having conserved pairs of Cys (-Tryptophan-Cystine-Glycine-Proline-Cystine-Lysine-) with a redox active S-S bridge, considered to be involved in defense against salt stress [13]. Mainly two types of thioredoxin systems have been found as plant mitochondrial and chloroplastic systems. A common system has been observed in mitochondria and chloroplast called thioredoxin/peroxiredoxin (Trx/Prx) comprising NADPH dependent thioredoxin reductase (NTR), glutaredoxin (GRX). These are involved in ROS metabolism and reduce H_2O_2 by acting as hydrogen donor and signals for plant salt stress responses [13,25]. Thiamine (Vitamin B1) as thiamine pyrophosphate (TPP) and thiamine diphosphate (TDP) acts as coenzyme in several metabolic pathways. El-Shintinawy et al. [73] reported that the addition of thiamine to the medium alleviated salt stress by increasing the contents of Cys and Met. Biotin (Vitamin H) also acts as coenzyme that catalyzes carboxylation, decarboxylation or transcarboxylation reactions and mediates salt tolerance [74]. CoA is a cofactor of many enzymatic reactions and is involved in salt tolerance. Yonamine et al. [75] observed that overexpression of HAL3A, a CoA biosynthetic genes alleviated salt stress in Arabidopsis.

The current focus on S assimilation has been to understand control of partitioning of S between primary and secondary metabolism [76], and the role of micro RNA (miRNA) families in plants in response to mineral nutrients limitation and to environmental stress. Using overexpression of Arabidopsis miRNA or expressing miRNA insensitive forms of the targets, scrutinizes the function of the miR395 in control of S nutrition or in indirect means to control the salt stress [77].

5. PHYTOHORMONES ACTION IN SALT TOLERANCE

The interconnected phytohormones signaling pathways are linked to various defense signaling pathways and are related to the developmental processes and metabolism of plants. The decline in endogenous levels of hormones has been related to the repressive effect of salt stress [78]. Thus, the contribution of exogenously applied CK, auxins, GA, ethylene, NO, JA and SA etc. have been shown to alleviate the negative effect of salt stress. Phytohormones such as Abscisic acid (ABA), IAA, CK, GA, JA are used for reducing or eliminating the negative effects of salt stress for adaptation [79] and SA for regulating the metabolic process as a function of antioxidative enzymes [5]. Exogenous application of Brassinosteroid (BR) and SA either to the seed before planting or to the growing plant, may overcome such deficiency and lead to a reduction in the inhibitory effects caused by the stress [80] probably by decreasing the accumulation of toxic Cl^- ions in leaves by ABA in citrus plants [81]. Pre soaking of seeds with optimal concentration of GA and SA has proved beneficial to growth and yield of some crop species grown under saline conditions by increasing nutrient reserves through increased physiological activities and root proliferation [82,83].

5.1 Phytohormones Signaling under Salt Stress

Phytohormones have regulatory effects on plant growth through its effect on cell division and extension and nullify the effects of abiotic stress on plant growth and development. In response to osmotic stress, tomato plants produce proteins which are induced by ABA [84]. Ethylene and auxin regulate cell wall protein expansin for the maintenance of root elongation [85] and root hair initiation for more effective water intake under salt stress [86]. Trivedi and Nath [87] found that *MaExp1* from ripening bananas could be upregulated by ethylene. Similarly, Rose et al. [88] found upregulation of an expansin in tomato by ethylene during fruit ripening. Ding et al. [89] found that IAA induced the expression of expansin genes including EXP-A and EXP-B; and Azeez et al. [90] identified that *GgEXPA1* is a gibberellins (GAs)-responsive expansin gene. The role of the DELLA proteins as potential integrators of phytohormone in the regulation of germination, cell redox state, growth, and stress responses is also worth mentioning [91]. DELLA proteins are repressors of GA signaling and also modulate ROS levels, involved in growth-regulatory mechanisms [92]. Li et al. [93] observed that constitutive overexpression of *TaEXPB23*, a wheat expansin gene increases the tolerance of transgenic tobacco under salt stress. It has been observed that synthesis of jasmonic-induced proteins (JIPs) takes place on JA treatment that aid in salt tolerance [10]. JA-dependent gene activation involves hormone-induced degradation of a transcriptional repressor, the jasmonate ZIM/tify-domain (*JAZ/TIFY*) proteins [94] in which 12 *JAZ/TIFY* genes have been identified in *Arabidopsis thaliana* [95]. The application of JA can mimick the effect of salt stress on the induction of *JAZ/TIFY* transcripts (repressor proteins) and cope with/adapt with their adverse function [96]. SA plays an important role in the control of gene expression and most of the genes encoding chaperone, heat shock proteins (HSPs), antioxidants and genes involved in secondary metabolites biosynthesis show SA signaling pathways in response to stress [97]. Furthermore, SA stimulates MAPK in tobacco cell cultures [98] which mediate responses to a variety of extracellular stimulus. It has been found that overexpression of *OsMAPK5* reduces salt stress in rice [99], whereas expression of *PsMAPK3* alters on the application of SA and decreases salt stress in pea plants [100].

Auxin affects various aspects of plant growth and development as well as regulation of gene expression. Jung et al. [101] showed a link between salt stress and seed germination protection by using auxin in Arabidopsis. Their observations indicate that NTM2 incorporates auxin signals into salt stress signaling during seed germination, suggesting a role of auxin in modulating seed germination under high salt stress. Auxin signals are also integrated via the overexpression of *IAA30* gene into the NTM2-mediated salt signaling pathway [102]. Exogenous IAA showed high stimulatory effect on the root and shoot growth of wheat seedling in saline condition [103]. Tirkayi et al. [104] observed that auxin signaling gene *axr1* played a role in protecting *Arabidopsis thaliana* from salt stress. Auxin increased hypocotyl length, seedling fresh and dry weight and hypocotyl dry weight of wheat cultivars under salt stress [105]. Fang et al. [106] reported that a number of auxin responsive gene (*AtMEKK1, AtRSH3, Cat1, Fer1*) expressions were downregulated and *NIT1, NIT2* were induced in *Arabidopsis thaliana* to alter the level of IAA and to interact with the responses of salt stress.

GA has also been found to alleviate harmful impacts of salt stress [107] by establishing better seedling growth and shoot and root biomass. GA application increased length and dry mass of soybean plants under salt stress by regulating the levels of GA and maintained normal growth and development [108] and reversed the inhibitory effects of salt on germination and seedling establishment of Arabidopsis [109] through its effect on source-sink relations for adjustment under environmental stress conditions [110]. Also, GA application reverses the effect of salt stress by decreasing proline content [111]. Alonso et al. [109] have shown that seed germination and seedling establishment of the FsGASA4 transgenic plants overexpressing a GA-responsive gene from beechnut (*Fagus sylvatica*), coding for a member of the GASA family (FsGASA4), are resistant to high salt, oxidative and heat stresses. Kaya et al. [112] noticed that salt inducible *DDF1* gene improved seed germination by altering GA level under salt stress. The effects of GA for salt tolerance include increase in reducing sugars, sucrose; increase in protein synthesis; decrease in activities of ribonuclease [113]; increase in the activitiy of antioxidant enzymes [111,114].

Nishiyama et al. [115] demonstrated that the upregulation of NAC genes might alter the morphological phenotype of CK-deficient plants, highlighting the impact of CK regulation on stress-responsive signaling pathways and adaptation to high salinity. In another study, Vyroubalova et al. [116] have shown that salt stress induces the expression of CK biosynthetic genes in maize seedlings and increases the active form of CK levels to acclimatize the stress.

ABA acts as a mediator in plant salt stress responses. Wang et al. [117] observed that ABA stimulus characterized the *ZmMPK3* genes from maize leaves and showed rapid activation on salt stress signaling. ABA has also been shown to be major internal signal in wheat plants to survive under salt stress conditions [118]. Li et al. [119] have observed that salt responsive gene *TaDi19A* from wheat increases the expression of ABA signal genes *ABI1, RAB18, ERD15, and ABF3* to improve salt tolerance.

Ethylene has long been regarded as a stress-hormone and linked with salt stress. The cell viability is determined by ethylene generated ROS and NO balance. Ethylene-regulated ROS and NO under salt stress in tomato cell suspension culture have been shown [120]. Ethylene and ethylene signaling pathway or receptor factor (ERF) enable plants to survive under adverse environmental conditions such as salt stress by suppressing salt sensitivity. A novel orthologue of ethylene response factor *MsERF11*, a salt-hormone-responsive gene, has the potential for improving salt tolerance in plants. However, overexpression of *MsERF11*in alfalfa plant is still needed to prove its full utility as a molecular breeding tool [121]. Cao et al. [122] established a link between ethylene signaling pathway and salt stress. Ethylene signaling interacts with SA and/or JA, resulting in the expression of a large array of defense genes [123]. Downstream of the multiple interactions between different defense pathways and transcriptional factors display very important roles in regulating the expression of functional genes such as coordination of *EIN3-ESE1* under salt stress. Zhang et al. [124] have reported that ERF gene (*ESE1*) was a downstream component in salt response, induced by ethylene and salt to build the transcriptional complex of *EIN3-ESE1*. Chuang et al. [125] also suggested a hairpin-induced-ethylene responsive factor that regulated tomato plant growth and salt stress in overexpressing *SlERF5* in Arabidopsis by activating a number of ethylene-responsive defense genes and modulating the ethylene and ABA-mediated gene expression to cope with the adverse environmental conditions. Seo et al. [126] have reported that overexpression of *BrERF4* gene from *Brassica rapa* species led to improved salt tolerance. In addition, Wang et al. [127] have shown that ethylene stimulates PM H^+ ATPase activity to modulate ion homeostasis to increase salt tolerance in Arabidopsis. Ethylene signaling modulates salt response at different levels, including membrane receptors, components in cytoplasm, and nuclear transcription factors in the pathway. Achard et al. [128] showed that ethylene signaling promoted salt tolerance in Arabidopsis. The analysis of Na^+/ K^+ homeostasis showed that K^+ nutrition was regulated by ethylene to improve salt tolerance in short-long term salt stressed plants. Ethylene signaling pathway involves ethylene receptors ETR1, ETR2, ERS1, ERS2, and EIN4 and another CTR1 (Constitutive Triple Response) in Arabidopsis, regulates downstream signaling and is considered to activate the expression of genes, resulting in responses to salt, drought and freezing stress [129]. The expression of *ETR1* gene seems to be downregulated by salt and osmotic stress at both transcription and protein levels in Arabidopsis [130]. Cao et al. [122] have shown that the gain-of-function mutant etr1-1, with ethylene insensitivity, showed increased sensitivity to salt stress during germination and early seedling development of Arabidopsis and on the opposite, the strong loss-of-function mutant etr1-7 showed increased tolerance to salt stress. Cao et al. [19] studied a subfamily II ethylene receptor *NTHK1* from tobacco and found that transgenic Arabidopsis and tobacco plants overexpressing the *NTHK1,* showed sensitivity to salt stress compared to wild type plants. Overexpression of the *NTHK1* gene or the receptor gain-of-function activated expression of salt-responsive genes *AtERF4* and *Cor6.6* and mutation of EIN2, a central component in ethylene signaling, also resulted in salt sensitivity, suggesting that EIN2-mediated signaling is beneficial for plant salt tolerance. Further, Cao et al. [131] reported that ethylene receptor *NTHK1* regulated ACC oxidase and ethylene responsive factor genes under salt stress and maintained differential ratio of Na^+/ K^+. Tobacco plants respond to a variety of environmental stresses through the induction of antioxidant defense enzymes that protect against further damage [132]. The EIN2 is a central membrane protein with 12 predicated transmembrane helices of ethylene signaling, which regulates salt stress response and interacts with a MA3 domain-containing protein *ECIP1* in Arabidopsis [133].

JA has been the focus of attention as a cellular growth regulator because of its ability to provide protection against salt stress on the productivity via plant signal transduction [10]. JA is an active member of the signal cascade involved in the induction of plant stress responses [134]. JA signaling has been extensively studied, using biochemical, molecular and genetical approaches in *Arabidopsis thaliana* and other species [95]. Moreover, JA is involved in diverse developmental processes such as seed germination, fruit growth, fertility, fruit ripening and senescence etc. Exogenous application of JA results in altered endogenous hormone level under salt stress. Kang et al. [135] reported that application of JA recovered salt inhibition on dry mass production in rice seedlings. In addition, ABA and JA work antagonistically and regulate the expression of salt stress-inducible proteins associated with defense responses [136].

NO appears to be present in most of the stress reactions and has protective functions [137,138]. NO activates different biochemical pathways via directly or indirectly interaction with proteins to produce metal proteins with heavy metals, S-nitrosylation with sulfuhydrl groups and nitro groups in the process of nitration to provide resistance against salt stress [139,140]. Similarly, the exogenous application of NO also protects chickpea leaves from NaCl-induced oxidative stress [141]. Guo et al. [142] suggested that NO might confer salt tolerance to *Kosteletzkya virginica* plants by preventing both oxidative membrane damage and translocation of Na^+ from roots to shoots. NO interacts with ROS and their homeostasis determines the fate of the cells [143]. NO produced under salt stress could serve as a second messenger for the induction of PM H^+-ATPase expression [130]. Zhang et al. [144] have reported that NO induced salt resistance of calluses from *Populus euphratica* under salt stress by increasing the K^+/Na^+ ratio, and this process was mediated by H_2O_2 and was dependent on the increased plasma membrane H^+-ATPase activity. NO functions as a signaling molecule in interaction with ROS, affects numerous physiological processes through the regulation of many genes in *Lupinus luteus* plants or functions as a regulator for gene expression [138]. Arabidopsis mutant *Atnoa1* with an impaired *in vivo* NOS activity and a reduced endogenous NO level was more sensitive to NaCl stress than the wild type [20]. Treatment with exogenous NO in the form sodium nitroprusside to *Atnoa1* alleviated the oxidative damage caused by NaCl stress, and instead, inhibition of NO accumulation in the wild type plants produced opposite effects. *Atnoa1* mutants displayed a greater Na^+/K^+ ratio in shoots than wild type when exposed to NaCl, but NO treatment attenuated this elevation of Na^+/K^+ ratio [20]. In this context, it has been shown that NO participates in salt stress and regulates the adverse effects. The potential ability of NO to scavenge H_2O_2 is due to the induction of subcellular antioxidant defense. NO significantly enhances the activities of SOD and CAT, both of which separately contribute to the delay of H_2O_2 accumulation and elevate ratio of GSH/GSSG and AsA/DHA in the wheat leaves to protect from oxidative damage caused by salt stress [145].

Exogenous application of SA has been shown to contribute in the regulation of physiological processes in mungbean plants such as growth, photosynthesis together with S and N metabolism [5]. SA reduces the adverse effects of salt stress effects in barley grains [146], in mungbean [53] and explains the protective role on membranes that increase the tolerance of plants to damage. Syeed et al. [22] have reported that SA induced salt tolerance in genetically diverse mustard plants explained different mechanisms of salt tolerance. Horvath et al. [147] have also found that membrane permeability and lipid oxidation which were increased by salt stress were lowered by SA. In addition to this, foliar application of SA significantly reduced NaCl toxicity effects by decreasing Na^+ and increasing K^+ and Mg^{2+} in the roots and shoots of tomato plants [148]. Rajjou et al. [149] observed that SA regulated the expression of *NahG* for the reponse to salt stress. Abreu and Munne-Bosch [150] used *NahG* (a bacterial NahG gene encoding SA hydroxylase) and SA-induction-deficient (sid2) mutants of Arabidopsis to assess the role of SA in plant development. It was suggested that the sid2 gene, which encodes isochorismate synthase played a key role in SA biosynthesis during Arabidopsis plant development and seed production. Lee et al. [151] have shown that the transcript levels of the *GA3ox1* gene were elevated in germinating wild-type seeds in the presence of 150 mM NaCl and 1 µM SA; and the regulation of GA and SA signals worked as positive feedback for seed germination under salt stress conditions. It has been shown that SA assists accumulation of both ABA and IAA in wheat seedlings under salt stress. It has been found that inhibition of CAT, an H_2O_2 scavenging enzyme, by SA plays a major role in the generation of ROS [147]. Nudix hydrolases genes are associated with detoxification processes in plants under abiotic stress and among their transcription levels, both*ClNUDX1* and *ClNUDX2* expressions were regulated by salt and SA [152] (Table 1).

Table 1. Phytohormones related gene expression in salt tolerance

Hormone	Gene/s Involved	Function and effect on salt tolerance	Plant	Reference
Auxin	*AtMEKKI, AtRSH3, Cat 1,Fer1* *NIT1, NIT2*	Auxin downregulates stress responsive genes *AtMEKKI, AtRSH3, Cat 1, and Fer1*. The expression of *NIT1, NIT2* induced by salt to alter IAA levels and increased salt tolerance.	Arabidopsis	[106]
	axr 1	*axr1* play role in auxin signalling and protection of plants from the inhibitory effect of salt stress and improves salt tolerance.	Arabidopsis	[104]
	IAA30	Overexpression of *IAA30* decreases salt tolerance through NTM2-mediated salt signalling	Arabidopsis	[102]

		cascade.		
Gibberellin	*npr1, ics1*	Exogenous application of gibberellins increases the expression level of *npr1*, *ics1* to improve salt tolerance via the involvement of salicylic acid biosynthesis and action.	Arabidopsis	[109]
Cytokinin	*CKX* genes (*CKX6,CKX, CKX10*)	Moderate increase in cytokonin levels acclimatizes the salt stress through induction of *CKXs* expression.	Maize	[116]
	NAC	Up regulation of *NAC* genes causes reduction in endogenous cytokinin levels and enhances salt tolerance.	Arabidopsis	[115]
Absicsic acid	*TaDi19A*	*TaDi19A* acts as positive regulator to upstream the expression of abscisic acid signal genes *ABI1, RAB18, ERD15, and ABF3* to improve salt tolerance.	Wheat	[119]
	TaSc	Overexpression of *TaSc* gene imparts higher salt tolerance by improving the expression of salt tolerant genes *AtFRY1, AtSAD1* and maintaining higher K^+/Na^+ ratio under ABA stimulus.	Arabidopsis	[40]
	ZmMPK3	ABA induces expression of *ZmMPK3* gene to play role in response to salt stress.	Maize	[117]
Ethylene	*NTHK1*	Ethylene receptor *NTHK1* gene regulates the gene expression of ACC oxidase (*NtACO3*) and ethylene responsive factor genes (*NtERF1* and *NtERF4*) under salt stress and maintains differential ratio Na^+/K^+ to improve salt tolerance.	Tobacco	[131]
	NTHK1	Overexpression of *NTHK1* activates the salt responsive genes *AtERF4, Cor6.6* and enhances salt tolerance.	Arabidopsis	[19]
	JERF3	*JERF3* expression regulates plant response to salt stress by modulating the level of ROS related genes, *NtSOD*, *NtCA* and enhances adaptation to salt.	Tobacco	[129]
	ETR1	Loss of function mutant etr1-7 shows increased salt tolerance.	Arabidopsis	[122]
	BrERF4	Overexpression of *BrER4* gene increases salt tolerance due to	Arabidopsis	[126]

		the suppression of salt-induced expressions of transcriptional repressor genes *ABI1, ABI2, AtPP2CA.*		
	SlERF5	Overexpression of *SlERF5* enhances salt tolerance by showing longer root growth and greener cotyledons.	Tomato	[125]
	SlERF1	Overexpression of *SlERF1* gene activates the expression of stress related genes (*LEA, P5CS, DREB3-1, ltpg2)* and enhances salt tolerance.	Tomato	[166]
	ECIP1	The expression of *ECIP1* gene interacts with EIN3 (ethylene signalling transcription factor) and regulates salt stress for tolerance.	Arabidopsis	[133]
	ESE1	The transcriptional complex of *ESE1* gene with EIN3 regulator activates the expression of salt-related genes and increases salt tolerance.	Arabidopsis	[124]
	MsERF11	Ethylene response factor gene *MsERF11* enhances salt tolerance via developmental and diverse pathways in salt stress response.	Arabidopsis	[121]
Jasmonate	*SalT, osdrr*	The expression of salt stress inducible transcript *SalT, osdrr* are accumulated under salt stress and antagonistically regulated by jasmonates and abscisic acid to associate with defense responses.	Rice	[136]
	JAZ/TIFY	*JAZ/TIFY* expression upstream jasmonate signalling in different level of jasmonate biosynthesis and induces the adaptation to salt stress.	Grapevines	[96]
Nitric oxide	*NOS1*	Reduction in endogenous NO content by inhibiting NOS by salt stress confers more sensitive to salt stress.	Arabidopsis	[20]
Salicylic acid	*NahG*	Salicylic acid regulates the expression of *NahG* and improves salt tolerance.	Arabidopsis	[149]
	PsMAPK3 *PR- 1b*	SA acts negatively and regulates higher expression of *PsMAPK3* and lowers *PR-1b* to suppress salt tolerance.	Pea	[100]

	CINUDXs	Salicylic acid regulates *CINUDXs,* show strong expression levels under salt to enhance salt tolerance.	Chrysanthemum	[152]

5.2 Phytohormones Regulate Sulfur Assimilation and Alleviate Salt Stress

There is increasing evidence of coordination between phytohormones and nutritional signaling. The involvement of phytohormones in S signaling and salt stress is a complex phenomenon as phytohormones may affect S availability and control gene expression related to S-metabolism (Fig. 1). The interaction between ROS and AsA-GSH cycle triggers the synthesis of phytohormones [153] which may signal plant response to nutrients deficiency. Phytohormones such as JA, ABA, SA, NO and ethylene play important roles in the accumulation of GSH under stress [60]. The regulation and function of GSH redox potential are integrated to fine-tune photo-respiratory and respiratory metabolism which modulate phytohormone signaling pathways through appropriate modification of sensitive protein Cys residues [25]. Therefore, there appears to be a requirement of phytohormones to cope with salt stress by antioxidant enzymes and for S regulation.

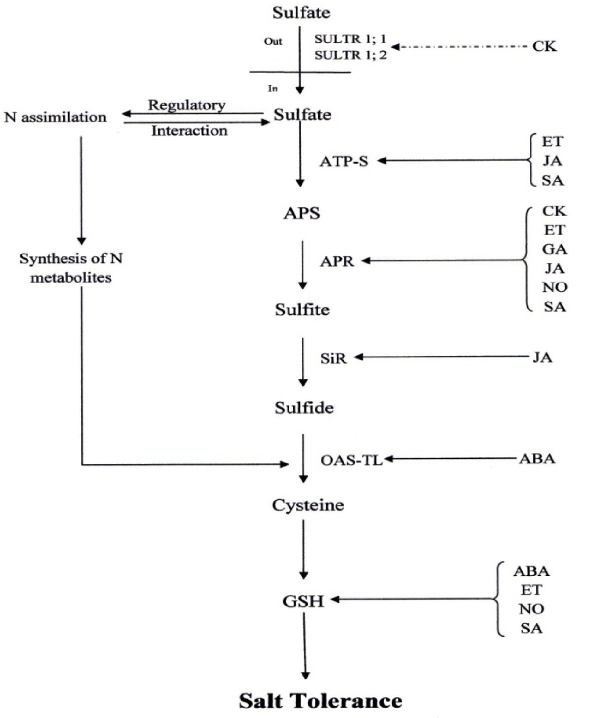

Fig. 1. Schematic representation of sulfur assimilatory pathway and possible regulatory events by phytohormones and nitrogen for salt stress tolerance. Arrow (—→) shows up-regulation of enzymes involved in sulfur assimilation pathway. Arrow (- - →) shows down-regulation of sulfur transporters. ATP-S; ATP sulfurylase, APR; adenosine 5' phosphosulfate reductase, ABA; abscisic acid, CK; cytokinin, ET; ethylene, GSH; reduced glutathione, JA; jasmonic acid, N; nitrogen, NO; nitric oxide, OAS-TL; *O*-acetylserine (thiol) lyase, S; sulfur, SA; salicylic acid, SiR; sulfite reductase, SULTR, sulfate transporter.

The interaction of auxin and S has been shown from the analysis of the transcriptional responses of *Arabidopsis thaliana* to S deficiency [154]. Sulfur deprivation activates transcription of several members of the Auxin/Indole-3-Acetic Acid (*Aux/IAA*) gene family and induces expression of *NIT3* (NITRI-LASE 3), a gene that encodes a key enzyme in the synthesis of auxin [154]. The deficiency of S triggers auxin repression presumably through Aux/IAA proteins [155]. On the other hand, auxin treatment inhibits expression of a low-S-responsive gene encoding a putative thioglucosidase, which likely releases thiol groups from glucosinolates, suggesting bi directionality in the S/auxin interaction [156]. However, the fact that low-S-induced expression of *SULTR1;2* and *APR2* is not affected by auxins indicates that auxins only control a subset of plant responses to S starvation. The expression of auxin-inducible genes (IAA18, At1g51950, tryptophan synthase β chain, At5g38530, putative auxin-regulated protein, At2g33830) is upregulated by S deficiency [157].

CK acts through the CK response receptor (CRE1) to regulate sulfate uptake and transporter expression. Maruyama-Nakashita et al. [158] reported that CK receptor (CRE1/WOL/ AHK4) was important for regulation given that the effect of CK was attenuated in cre1-1 mutants. CK repressed gene expression for high-affinity sulfate transporters *SULTR1;1* and *SULTR1;2*, accumulated under low-S conditions [158]. This repressing effect depended on the function of the CK receptor CRE1 and was correlated with limited sulfate uptake capacity of Arabidopsis roots. However, there is evidence showing that CK can also induce expression of genes that respond to S deprivation, as is the case of APR and *SULTR2;1* genes in Arabidopsis [64]. *SULTR2;1* corresponds to a low-affinity sulfate transporter whereas APR genes encode adenosine 5-phosphosulfate reductase, a key enzyme in the S assimilation pathway whose expression is induced by NaCl and reduced by N deficiency or treatment with thiols, indicating that the enzyme also integrates signaling from stimuli other than nutritional stresses [68]. Although NaCl-induced expression of the APR genes was observed in Arabidopsis mutants with reduced CK accumulation or perception, this effect did not correlate with increased APR protein and activity [57]. Together, these studies indicate that CK plays different and complex roles, at both the transcriptional and posttranscriptional level in the control of S signaling.

ABA plays an important role in adaptive responses to environmental stresses and induces mRNA accumulation of cytosolic OASTL. Chen et al. [159] reported that the accumulation of ABA induces negative role of *AtGSTUI7* in stress tolerance by affecting GSH pool. It seems that this compound may have a more profound effect on control of S metabolism under stress conditions [61]. ABA is also known to impact S homeostasis by increasing the levels of GSH, an intermediary in S metabolism that plays a critical role in maintaining the redox state of Arabidopsis plants [160]. ABA regulates the expression of *OsMCSU* in rice and maintains the level of ABA [161]. Therefore, ABA-mediated control of ROS levels has been invoked to explain its function in protecting plants against oxidative conditions caused by many stress situations, including nutritional deficiencies.

Ethylene plays a role in the regulation of synthesis of S compounds through SAM and controls the regulation of plant processes and stress tolerance [12]. Burstenbinder et al. [162] showed that Yang cycle contributed to SAM homeostasis using an *mtk* mutant, especially when *de novo* SAM synthesis was limited, such as at S deficiency [163]. Ethylene and JA signaling pathway prevented GSH accumulation under salt stress, but in the absence of ethylene signaling, GSH would not accumulate signifying that components of GSH biosynthesis are under the control of ethylene [57]. Ethylene has been shown to regulate S availability and GSH synthesis for stress tolerance [164]. Moreover, application of ACC (ethylene precursor) results in the increased accumulation of APR activity. Recently, it has been shown that ethylene action in mustard is dependent on S availability [164,165]. Wu et al. [129] reported that transcriptional activation of ethylene responsive factors (ERF) in ethylene signaling process enhanced stress tolerance in tobacco seedlings by decreasing ROS accumulation in response to salt, drought and freezing. Similarly, Lu et al. [166] observed that *SlERF1* played a positive role in the salt tolerance of tomato plants.

JA transcriptional responses have revealed that a significant number of genes controlling S metabolism (16 out of 100 genes tested) respond to treatments with JA and at least two-fold changes in their mRNA expression were observed [167]. Among these, 13 and 3 genes were upregulated or down-regulated, respectively, suggesting that JA treatment has mainly a positive effect on S metabolism. Conversely, a large number of JA biosynthesis genes were induced under low-S conditions [154,157]. Additionally, methyl jasmonate is involved in regulating the activity of S assimilation enzymes such as SAT and APR [167]. An ethylene insensitive like (EIL) transcription factor, *SLIM1*, was isolated and shown to be involved in the regulation of a high-affinity sulfate transporter in response to sulfate limitation [168]. JA acts in a dose-dependent manner in the regulation of GSH synthesis especially when mRNAs for sulfate assimilation enzymes are increased. JA induces GSH1, GSH2 and GR [169]. The interaction of JA and GSH induces resistance to *Botrytis cinerea*, an effect that was partly or wholly suppressed in GSH-deficient mutants [170]. The SA-inducible protein, GRX480, represses up-regulation of certain JA-induced genes [171]. Gene expression profiles and SA contents suggest that the more oxidized GSH status in *gr1* is associated with repression of both SA and JA pathways, and therefore the role of GSH may be complex and not limited to regulating antagonism between the two hormones [153]. Several GSTs are among early JA-induced genes, which catalyze formation of GS-oxylipin conjugates [172]. Methyl jasmonate treatment resulted in a fast but transient increase in mRNA levels of many genes involved in sulfate assimilation and GSH synthesis, but without affecting S metabolite levels in Arabidopsis [167].

Nitric acid metabolism in higher plants is involved in a wide range of processes such as cellular signaling and response mechanisms against adverse stress conditions. The analysis of GSNOR (a product of GSH and NO under stress) protein and activity in Arabidopsis by immunolocalization and histochemical methods showed that this protein is differentially expressed. Moreover, in transgenic Arabidopsis plants, both overexpressing and knock-down GSNOR had a short-root phenotype that was correlated with a lowering of the intracellular GSH level and an alteration in its spatial distribution in the roots, suggesting that GSNOR might be involved in the regulation of redox state [140]. Several roles have been attributed to the extracellular ATP (eATP) and NO in plants, ranging from cell viability to pathogen defense and cell death. It has been demonstrated that a fine-modification of redox balance and endogenous NO level are associated to ATP action. GSH-mediated inhibition of etiolated hypocotyl growth and rooting in lupin was observed by Cano et al. [173] and inter connection between eATP, NO and redox system during hypocotyl elongation in etiolated Arabidopsis seedlings [174]. More recently, Terrile et al. [175] demonstrated that in the presence of GSH, etiolated Arabidopsis seedlings showed inhibition of hypocotyl elongation and altered root system architecture including changes in primary root length, root hair number and agravitropic growth, and all these morphological traits were restored by ATP and GSH. In addition to this, Terrile et al. [175] have reported that NO influences auxin signaling through S-nitrosylation of the Arabidopsis transport inhibitor 1 auxin receptor. Extracellular ATP-NO action on GSH-treated seedlings grown in darkness is restricted not only to hypocotyl elongation but also to root hair development. A balance between eATP and NO is tightly regulated possibly by impairing auxin transport because NO is involved in auxin-induced root hair formation [176]. Indeed, redox-dependent modulation by eATP and NO signaling may be an adaptive strategy under environmental stress conditions [177].

The significance of thiol-disulphide is its involvement in the regulation of SA-dependent Non expressor of Pathogenesis-Related Genes 1 (*NPR1*) pathway [178]. Activation of *NPR1* involves a reductive change; the initial trigger for the events leading to PR gene expression. Similar changes have also been reported subsequent to exogenous application of the defense related hormone SA, or biologically active SA analogs [179]. Whether SA regulates the expression of *γECS and GSHS*, it affects SAT or it utilizes another mechanism to increase GSH synthesis remain to be elucidated. Enhancement in GSH content and redox state under salt stress has been observed, which alleviates the negative effects of salt stress on photosynthesis depending on the concentration of SA application [5]. The higher synthesis of GSH in turn affects the level of antioxidant enzymes. SA-treated mustard plants exhibited changes in the physiological processes to maximize the use efficiency of N and S through higher activity of nitrate reductase (NR) and ATPS and synthesis of GSH [22] (Table 2).

Table 2. Mediation of phytohormones in genes involved in sulfur responses

Hormone	Gene/s involved	Function and effect on sulfur response	Plant	Reference
Auxin	*SULTR1;2, SULTR4;1*	Auxin application overexpresses *SULTR1;4, SULTR4;1* under sulfur starvation to provide the direct cross-talk of the auxin biosynthesis pathway with the sulfur assimilation pathway.	Arabidopsis	[154]
	At2g44460, APR2, SULTR1;2	Auxin suppresses the expression of *At2g44460* (thioglucosidase gene) but not that of *SULTR1;2and APR2* so as to participate in remobilizing sulfur from the intracellular storage on sulfur deficiency.	Arabidopsis	[157]
Gibberellin	*APR1, APR2*	Gibberellins regulate the accumulation of *APR1, APR2* transcripts.	Arabidopsis	[68]
Cytokinin	*APR1, SULTR2;2*	Cytokinins upregulates the expression of *APR1, SULTR2;2* genes through an increase in sucrose concentrations and suggest roles in the regulation of sulfur assimilation.	Arabidopsis	[64]
	SULTR1; 1, SULTR1; 2	Cytokinins downregulate the expression of *SULTR1;1, SULTR1;2* with the decrease in sulphate uptake activities in roots through involvement of CRE/WOL/AHK4-derived signal.	Arabidopsis	[158]
Abscisic acid	*AtGSTUI7*	Accumulation of ABA induces negative role of *AtGSTUI7* in stress tolerance by affecting	Arabidopsis	[159]

		GSH pool.		
	OsMCSU	ABA regulates the expression of *OsMCSU*. The molybdenum cofactor sulfurase (MCSU) that transfers the sulfur ligand to aldehyde oxidase-bound MoCo is considered an important factor in regulating the ABA levels in plant tissues.	Rice	[161]
Ethylene	*APR1, APR3*	Ethylene increases the accumulation of *APR1, APR3* transcripts.	Arabidopsis	[68]
Jasmonate	*APS2, APR3,ATPS, SIR,SAT3,γECS*	Methyl jasmonate upregulates the expression of sulfur assimilation pathway responsive genes *APS2, APR3,ATPS, SIR,SAT3,γECS.*	Arabidopsis	[167]
	APR1, APR3	Jasmonates increase the accumulation of *APR1,APR3* transcripts.	Arabidopsis	[68]
	PDF1.2	*PDF1.2* gene is dependent upon Jasmonates whom expression is suppressed by GRX480 transcription.	Arabidopsis	[171]
Nitric oxide	*NPR1 (via GSNO and TRXs*)	Nitric oxide in the form of GSNO directs the function of *NPR1* gene in the defense response with TRXs(thioredoxins).	Arabidopsis	[178]
Salicylic acid	*γECS, GSHS*	Salicylic acid regulates the expression of *γECS, GSHS* to increase the level of GSH synthesis.	Arabidopsis	[61]
	APR1, APR2, APR3	Salicylic acid increases mRNA levels of all *APR1,APR2,APR3.*	Arabidopsis	[68]

6. CONCLUSION

Salt tolerance is a complex phenomenon in plants, and various research methodologies and genetic approaches are used to characterize the diverse biochemical events that occur in response to salt stress. Based on the knowledge of enhanced expression of a number of functionally related genes and activities of antioxidant enzymes, plants can be protected from oxidative stress damages. Sulfur plays key roles in the primary metabolism of plants and provides structural components of essential cellular molecules. Sulfur-mediated regulation serves as a major determinant for depicting salt tolerance. In plants, assimilation of sulfate provides signals for the formation of Cys, an immediate precursor for the synthesis of GSH which is involved in protection of plants against salt stress by alleviating the salt-induced oxidative stress. Additionally, an improved knowledge of the underlying mechanisms of action of exogenously applied phytohormones is useful to return metabolic activities to their normal levels under salt stress conditions. Moreover, phytohormones have been shown to be beneficial for the physiology and metabolism of plants under salt stress, since it provides a mechanism to regulate the metabolic process as a function of antioxidative enzymes.

Coordination between S and hormonal signals controls plant growth, development and metabolism under salt stress conditions. S assimilates in plants act as signaling molecules for cellular communication with the environment and hormones and exhibit changes in all physiological processes to maximize the use efficiency of S. The literature reviewed demonstrates the effects of phytohormones signaling on the regulation of sulfate assimilation GSH synthesis, physiological processes and productivity of crop species under salt stress.

FUTURE PERSPECTIVES

To understand how plants coordinate multiple hormonal components with S assimilation in response to various developmental and environmental cues is a major challenge for the future. Therefore, the response of plants to phytohormones in enhancing/strengthening salt tolerance involving mineral nutrients at biochemical and molecular level is needed. Future strategies can be focused on how to decipher the interaction of phytohormones in modulating the S assimilatory enzymes under salt stress and detailed studies can be carried out on the molecular regulation of enzyme activities in different plant tissues. Currently, research has been more concentrated on Cys and GSH role in salt tolerance and other S-containing compounds are not studied under salt stress. It is also required to focus our attention on the involvement of other S-containing compounds in alleviation of salt stress and to look at how much these compounds are induced by phytohormones. The integrated approach from other disciplines of plant sciences such as physiology, biochemistry, molecular biology and genetic engineering towards better understanding of the mechanisms involved in salt tolerance induced by S and phytohormones would help in solving the problem.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

REFERENCES

1. Food and Agricultural Organization, FAO. Land and plant nutrition management service; 2008. Available: http://www.fao.org/ag/ag1/ag11/spush/.
2. Manchanda G, Garg N. Salinity and its effect on the functional biology of legumes. Acta Physiol Plant. 2008;30:595-18.
3. Ghogdi EA, Izadi-Darbandi A, Borzouei A. Effects of salinity on some physiological traits in wheat (*Triticum aestivum* L.) cultivars. Ind J plant Sci. 2012;5:1901-06.
4. Fageria NK, Baligar VC, Li LC. The role of nutrient efficient plants in improving crop yields in the twenty first century. J Plant Nutr. 2008;31:1121-57.

5. Nazar R, Iqbal N, Syeed S, Khan NA. Salicylic acid alleviates decreases in photosynthesis under salt stress by enhancing nitrogen and sulfur assimilation and antioxidant metabolism differentially in two mungbean cultivars. J Plant Physiol. 2011;168:807-15.
6. Sharma P, Jha AB, Dubey RS, Pessarakli M. Oxidative stress and antioxidative defense system in plants growing under abiotic stresses. In: Pessarakli M editor. Handbook of Plant and Crop Stress. 3rd ed. Taylor and Francis: USA. 2010;89-138.
7. Sharma P, Jha AB, Dubey RS, Pessarakli M. Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. J Bot. 2012;1-26.
8. Turan S, Tripathy BC. Salt and genotype impact on antioxidative enzymes and lipid peroxidation in two rice cultivars during deetiolation. Protoplasma. 2013;250:209-22.
9. Nazar R, Iqbal N, Masood A, Syeed S, Khan NA. Understanding the significance of sulfur in improving salinity tolerance in plants. Environ Exp Bot. 2011b;70:80-7.
10. Khan MIR, Syeed S, Nazar R, Anjum NA. An Insight into the Role of Salicylic Acid and Jasmonic Acid in Salt Stress Tolerance. In : Khan N, Nazar R, Iqbal N, Anjum N, editors. Phytohormones and abiotic stress tolerance in plants. Springer Heidelberg Dordrecht: London, New York; 2012;277-300.
11. Marschner H. Mineral Nutrition of Higher Plants. Academic Press, London; 1995.
12. Iqbal N, Masood A, Khan MIR, Asgher M, Fatma M, Khan NA. Cross-talk between sulfur assimilation and ethylene signaling in plants. Plant Signal Behav. 2013;8:1-9.
13. Khan MIR, Asgher M, Iqbal N, Khan NA. Potentiality of sulphur-containing compounds in salt stress tolerance. In: Ahmad P, Azooz MM, Prasad MNV, editors. Ecophysiology and responses of plants under salt stress. Springer: New York. 2013;443-72.
14. Kim H, Hirai MY, Hayashi H, Chino M, Naito S, Fujiwara T. Role of O-acetyl-L-serine in the coordinated regulation of the expression of a soybean seed storage protein gene by sulfur and nitrogen nutrition. Planta. 1999;209:282-89.
15. Szalai G, Kellos T, Galiba G, Kocsy G. Glutathione as an antioxidant and regulatory molecule in plants under abiotic stress conditions. J Plant Growth Regul. 2009;28:66-80.
16. Gul B, Khan MA, Weber DJ. Alleviation salinity and dark enforced dormancy in *Allenrolfea occidentalis* seeds under various thermoperiods. Aust J Bot. 2000;48:745-52.
17. Khan MA, Gul B, Weber DJ. Action of plant growth regulators and salinity on seed germination of *Ceratoides lanata*. Can J Bot. 2004;82:37-42.
18. Afzal I, Basra S, Iqbal A. The effect of seed soaking with plant growth regulators on seedling vigor of wheat under salinity stress. J Stress Physiol Biochem. 2005;1:6-14.
19. Cao WH, Liu J, He XJ, Mu RL, Zhou HL, Chen SY, Zhang JS. Modulation of ethylene responses affects plant salt-stress responses. Plant Physiol. 2007;143:707-19.
20. Zhao MG, Tian QY, Zhang WH. Nitric oxide synthase-dependent nitric oxide production is associated with salt tolerance in Arabidopsis. Plant Physiol. 2007;144:206-17.
21. Yoon JY, Hamayun M, Lee IJ. Methyl jasmonate alleviated salinity stress in soyabean. J Crop Sci Biotechnol. 2009;12:63-8.
22. Syeed S, Anjum NA, Nazar R, Iqbal N, Masood A, Khan NA. Salicylic acid-mediated changes in photosynthesis, nutrients content and antioxidant metabolism in two mustard (*Brassica juncea* L.) cultivars differing in salt tolerance. Acta Physiol Plant. 2011;33:877-86.
23. Velitcukova M, Fedina I. Response of photosynthesis of *Pisum sativum* to salt stress as affected by methyl jasmonate. Photosynthetica 1998;35:89-97.

24. Wen F, Zhang Z, Bai T, Xu Q, Pan Y. Proteomics reveals the effects of gibberellic acid (GA3) on salt-stressed rice (*Oryza sativa* L.) shoots. Plant Sci. 2010;178:170-75.
25. Noctor G, Mhamdi A, Chaouch S, Han Y, Neukermans J, Marquez-Garcia B, Queval G, Foyer CH. Glutathione in plants: an integrated overview. Plant Cell Environ. 2012;35:454-84.
26. Tanou G, Molassiotis A, Diamantidis G. Induction of reactive oxygen species and necrotic death-like destruction in strawberry leaves by salinity. Environ Exp Bot. 2009;65:270-81.
27. Rodriguez MC, Petersen M, Mundy J. Mitogen activated protein kinase signaling in plants. Annu Rev Plant Biol. 2010;61:621-49.
28. Xing Y, Jia W, Zhang J. AtMKK1 mediates ABA-induced CAT1 expression and H_2O_2 production via AtMPK6-coupled signaling in Arabidopsis. Plant J. 2008;54:440-51.
29. Droillard MJ, Boudsocq M, Barbier-Brygoo H, Lauriere C. Involvement of MPK4 in osmotic stress response pathways in cell suspensions and plantlets of *Arabidopsis thaliana*: activation by hypo osmolarity and negative role in hyperosmolarity tolerance. FEBS Lett. 2004;574:42-8.
30. Ding HD, Zhang XH, Xu SC, Sun LL, Jiang MY, Zhang AY, Jin YG. Induction of protection against paraquat-induced oxidative damage by abscisic acid in maize leaves is mediated through mitogen-activated protein kinase. J Integr Plant Biol. 2009;51:961-72.
31. Munns R, Tester M. Mechanisms of salinity tolerance. Annu Rev Plant Biol. 2008; 59:651-81.
32. Verslues PE, Batelli G, Grillo S, Agius F, Kim YS, Zhu J, Agrawal M, Katiyar-Agrawal S, Zhu JK. Interaction of SOS 2 with nucleoside diphosphate kinase 2 and catalases reveals a point of connection between salt stress and H_2O_2 signaling in *Arabidopsis thaliana*. Mol Cell Biol. 2007;27:7771-80.
33. Batelli G, Verslues P, Agius F, Qiu Q, Fujii H, Pan S, Schumaker K, Grillo S, Zhu J. Promotes salt tolerance in part by interacting with the vacuolar H+-ATPase and upregulating its transport activity. Mol Cel Biol. 2007;27:7781-90.
34. Gill SS, Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant Physiol Biochem. 2010;48:909-30.
35. Tausz M, Sircelj H, Grill D. The glutathione system as a stress marker in plant ecophysiology: is a stress-response concept valid. J Exp Bot. 2004;55:1955-62.
36. Ferreira-silva SL, Voigt EL, Silva EN, Maia JM, Aragão TCR, Silveira ACG. Partial oxidative protection by enzymatic and non-enzymatic components in cashew leaves under high salinity. Biologia Plantar. 2012;56:172-76.
37. Jithesh MN, Prashanth SR, Sivaprakash KR, Parida AK. Monitoring expression profiles of antioxidant genes to salinity, iron, oxidative, light and hyperosmotic stresses in the highly salt tolerant grey mangrove, *Avicennia marina* (Forsk.) Vierh by mRNA analysis. Plant Cell Rep. 2006;25:865-76.
38. Wang Y, Wang T, Li K, Li X. Genetic analysis of involvement of *ETR1* in plant response to salt and osmotic stress. Plant Growth Regul. 2008;54:261-69.
39. Lisa L A, Elias SM, Rahman MS, Shahid S, Iwasaki T, Hasan AM , Kosuge K, Fukami Y, Seraj ZI. Physiology and gene expression of the rice landrace Horkuch under salt stress. Funct Plant Biol. 2011;38:282-92.
40. Huang X, Zhang Y, Jiao B, Chen G, Huang S, Guo F et al. Overexpression of the wheat salt tolerance-related gene *TaSC* enhances salt tolerance in Arabidopsis. J Exp Bot. 2012;63:5463-73.
41. Yang G, Chen X, Tang T, Zhou R, Chen S , Li W, Ouyang J, He L, Shi S. Comparative genomics of two ecologically differential populations of *Hibiscus tiliaceus* under salt stress. Funcnl Plant Biol. 2012;38:199-208.

42. Ashraf M, Foodlad MR. Crop breeding for salt tolerance in the era of molecular markers and marker-assisted selection. Plant Breeding. 2013;132:10-20.
43. Vuylsteke M, Peleman JD, van Eijk MJT. AFLP-based transcript profiling (cDNA-AFLP) for genome-wide expression analysis. Nature Proto. 2007;2:1399-1413.
44. He H, Yajing N , Huawen C, Xingjiao T, Xinli X, Yin Weilun Y et al. cDNA-AFLP analysis of salt-inducible genes expression in *Chrysanthemum lavandulifolium* under salt treatment. J Plant Physiol. 2012;169:410-20.
45. Baisakh N, Subudhi P, Parami N. cDNA-AFLP analysis reveals differential gene expression in response to salt stress in a halophyte *Spartina alterniflora* Loisel. Plant Sci. 2006;170:1141-49.
46. Rodriguez-Uribe L, Higbie S, Stewart J, Wilkins T, Lindemann W, Sengupta-Gopalan C, Zhang J. Identification of salt responsive genes using comparative microarray analysis in upland cotton (*Gossypium hirsutum* L.). Plant Sci. 2011;180:461-69.
47. Seki M, Narusaka M, Ishida J, Nanjo T, Fujita M. Monitoring the expression profiles of 7000 Arabidopsis genes under drought, cold, and high-salinity stresses using a full-length cDNA microarray. Plant J. 2002;31:279-92.
48. Zsingmond L, Szepesi A, Trai I, Gabor R, Annamaria K, Laszlo S. Overexpression of the mitochondrial *PPR40* gene improves salt tolerance in Arabidopsis. Plant Sci. 2012;182:87-93.
49. Altman A, Vinocur BJ, Shoseyov O. SP1, a novel stress- associated , is symoylated upon salt stress in *Populus eupharitica*, and in consequently relocated from the cytosol to the plasma membrane and to the nucleus. Plant Abiotic Stress -from signaling to development. Tartu: Estonia; 2009.
50. Tuteja N. Cold, salt and drought stress. In: Hirt H, editor. Plant Stress Biology: From Genomics towards System Biology. Wiley-Blackwell and Weinheim: Germany. 2010:137-59.
51. Zhou M, Ma J, Zhao Y , Zhao YM, Wei YH, Tang YX, Wu YM. Improvement of drought and salt tolerance in Arabidopsis and *Lotus corniculatus* by overexpression of a novel DREB transcription factor from *Populus euphratica*. Gene. 2012;506:10-7.
52. Pandolfi C, Mancuso S, Shabala S. Physiology of acclimation to salinity stress in pea (*Pisum sativum*). Environ Exp Bot. 2012;84:44-51.
53. Khan NA, Syeed S, Masood A, Nazar R, Iqbal N. Application of salicylic acid increases contents of nutrients and antioxidative metabolism in mungbean and alleviates adverse effects of salinity. Int J of Plant Biol. 2010;1:1-8.
54. Saeid AR, Suwwan M. Effect of phosphorus on osmotic-stress responses of cucumber microshoots. Advances Environ Biol. 2012;6:1626-32.
55. Astolfi S, Sabrina. Adequate S supply protects barley plants from adverse effects of salinity stress by increasing thiol contents. Acta Physiol Plant. 2013;35:175-81.
56. Anjum NA, Gill SS, Umar S, Ahmad I, Duarte AC, Pereira E. Improving Growth and Productivity of *Oleiferous Brassicas* under changing environment: Significance of nitrogen and sulphur nutrition, and underlying mechanisms. Scientific World J. 2012: 657808.
57. Koprivova A, Kopriva, S. Lessons from investigation of regulation of APS reductase by salt stress. Plant Signal Behav. 2008;8:567-69.
58. Abdallah ML, Dubousset F, Meuriot P, Etienne JC, Avice, Ourry A. Effect of mineral sulphur availability on nitrogen and sulphur uptake and remobilization during the vegetative growth of *Brassica napus* L. J Exp Bot. 2010;61:2635-46.
59. Lappartient A, Touraine B. Demand driven control of root ATP sulfurylase activity and sulfate uptake in intact canola. Plant Physiol. 1996;111:147-57.

60. Kopriva S, Rennenberg H. Control of sulphate assimilation and glutathione synthesis: interaction with N and C metabolism. J Exp Bot. 2004;55:1831-42.
61. Kopriva S. Regulation of sulfate assimilation in Arabidopsis and beyond. Ann Bot. 2006;97:479-95.
62. Smith FW, Ealing PM, Hawkesford MJ, Clarkson DT. Plant members of a family of sulfate transporters reveal functional subtypes. Proc Natl Acad Sci (USA). 1995;92:9373-77.
63. Vauclare P, Kopriva S, Fell D, Suter M, Sticher L, von Ballmoos P, Krahenbuhl U, Op den Camp R, Brunold C. Flux control of sulphate assimilation in *Arabidopsis thaliana*: adenosine 5′-phosphosulphate reductase is more susceptible to negative control by thiols than ATP sulphurylase. Plant J. 2002;31:729-40.
64. Ohkama N, Takei K, Sakakibara H, Hayashi H, Yoneyama T, Fujiwara T. Regulation of sulfur-responsive gene expression by exogenously applied cytokinins in *Arabidopsis thaliana*. Plant Cell Physiol. 2002;43:1493-1501.
65. Koprivova A, Suter M, Op den Camp R, Brunold C, Kopriva S. Regulation of sulfate assimilation by nitrogen in Arabidopsis. Plant Physiol. 2000;122:737-46.
66. Khan NA, Nazar R, Anjum NA. Growth, photosynthesis and antioxidant metabolism in mustard (*Brassica juncea* L.) cultivars differing in ATP-sulfurylase activity under salinity stress. Sci Hort. 2009;122:455-60.
67. Ruiz JM, Blumwald E. Salinity-induced glutathione synthesis in *Brassica napus*. Planta. 2002;214:965-69.
68. Koprivova A, North KA, Kopriva S. Complex signaling network in regulation of adenosine 5’-phosphosulfate reductase by salt stress in Arabidopsis roots. Plant Physiol. 2008b;146:1408-20.
69. Lopez-Berenguera C, Carvajala M, Garcea-Viguerab C, Alcaraz CF. Nitrogen, phosphorus, and sulfur nutrition in Broccoli plants grown under salinity. J Plant Nutr. 2007;30:1855-70.
70. Aono M, Kubo A, Saji H, Tanaka K, Kondo N. Enhanced tolerance to photooxidative stress of transgenic *Nicotiana tabacum* with high chloroplastic glutathione reductase activity. Plant Cell Physiol. 1993;34:129-35.
71. Geu-Flores F, Nielsen MT, Nafisi M, Moldrup ME, Olsen CE, Motawia MS, Halkier BA. Glucosinolate engineering identifies a gamma-glutamyl peptidase. Nat Chem Biol. 2009;5:575-77.
72. Glaser HV, Thomas D, Gaxiola H. Salt tolerance and methionine biosynthesis in *Saccharomyces cerevisiae* involves a putative phosphatase gene. EMBO J. 1993;12:3105-10.
73. El-Shintinawy F, El-Shourbagy MN. Alleviation of changes in protein metabolism in NaCl-stressed wheat seed by thiamine. Biol Plant. 2001;44:541-45.
74. Hamdia M, Abd El-Samad. Physiological studies on the influence of biotin or pyridoxine in amelioration the effect of salinity in lupine plants. Bull Fac Sci Assiut Univ. 2000;29:283-91.
75. Yonamine I, Yoshida K, Kido K, Nakagawa A, Nakayama H, Shinmyo A. Overexpression of NtHAL3 genes confers increased levels of proline biosynthesis and the enhancement of salt tolerance in cultured tobacco cells. J Exp Bot. 2004;55:387-95.
76. Kopriva S, Mugford SG, Baraniecka P, Lee BR, Matthewman CA, Koprivova A. Control of sulfur partitioning between primary and secondary metabolism in Arabidopsis. Frontiers Plant Sci. 2012;3:1-9.
77. Matthewman CA, Kawashima CG, Húska D, Csorba T, Dalmay T, Kopriva S. miR395 is a general component of sulfate assimilation regulatory network in Arabidopsis. FEBS Lett. 2012;586:3242-48.

78. Debez A, Chaibi W, Bouzid S. Effect du NaCl et de regulatoeurs de croissance sur la germination d' *Atriplex halimus* L. Cah Agric. 2001;10:135-38.
79. Javid MG, Sorooshzadeh A, Moradi F, Sanavy SAMM, Allahdadi I. The role of phytohormones in alleviating salt stress in crop plants. Aust J Crop Sci. 2011;5:726-34.
80. Ashraf M, Akram N, Arteca R. The physiological, biochemical and molecular roles of brassinosteroids and salicylic acid in plant processes and salt tolerance. Cri Rev Plant Sci. 2010;3:162-90.
81. Gomez CA, Arbona V, Jacas J, PrimoMillo E, Talon M. Abscisic acid reduces leaf abscission and increases salt tolerance in citrus plants. J Plant Growth Regu. 2002;21:234-40.
82. Parida AK, Das AB. Salt tolerance and salinity effects on plants: a review. Ecotoxicol Environ Saf. 2005;60:324-49.
83. Liopa-Tsakalidi A, Kaspiris G, Salahas G, Barouchas P. Effect of salicylic acid (SA) and gibberellic acid (GA3) pre-soaking on seed germination of stevia (*Stevia rebaudiana*) under salt stress. J of Med Plants Res. 2012;6:416-23.
84. Jin S, Chen CCS, Plant AL. Regulation by ABA of osmotic-stress-induced changes in protein synthesis in tomato roots. Plant Cell Environ. 2000;25:51-60.
85. Yang L, Zheng B, Mao C, Qi X, Liu F, Wu P. Analysis of transcripts that are differentially expressed in three sectors of the rice root system under water deficit. Mol Genet Genomics. 2004;272:433-42.
86. Cho HT, Cosgrove DJ. Regulation of root hair initiation and expansin gene expression in Arabidopsis. Plant Cell. 2002;14:3237-53.
87. Trivedi PK, Nath P. MaExp1, an ethylene-induced expansin from ripening banana fruit NBRI, Plant Sci. 2004;167:1351-58.
88. Rose JKC, Lee HH, Bennett A. Expression of a divergent expansin gene is fruit-specific and ripening-regulated. Pro Natl Acad Sci U S A. 1997;94:5955-60.
89. Ding X, Cao Y, Huang L, Zhao J, Xu C, Li X, Wang S. Activation of the indole-3-acetic acid-amido synthetase GH3-8 suppresses expansin expression and promotes salicylate- and jasmonate-independent basal immunity in rice. Plant Cell. 2008;20:228-40.
90. Azeez AP, Sane SK, Tripathi D, Bhatnagar P, Nath. The gladiolus *GgEXPA1* is a GA-responsive alpha-expansin gene expressed ubiquitously during expansion of all floral tissues and leaves but repressed during organ senescence. Postharvest Biol Tec. 2010;58:48-56.
91. Grant MR, Jones JD. Hormone (dis)harmony moulds plant health and disease. Sci. 2009;324:750-52.
92. Achard P, Fan Gong,Soizic Cheminant,Malek Alioua,Peter Hedden,and Pascal Genschik. The cold-inducible CBF1 factor–dependent signaling pathway modulates the accumulation of the growth-repressing DELLA proteins via Its effect on gibberellin metabolism. The Plant Cell. 2008;20:2117-29.
93. Li F, Xing S, Guo Q, Zhao M, Zhang J, Guo Q, et al. Drought tolerance through overexpression of the expansin gene*TaEXPB23* in transgenic tobacco. J Plant Physiol. 2011;168:960-66.
94. Vanholme B, Grunewald W, Bateman A, Kohchi T, Gheysen G. The tify family previously known as ZIM. Trends Plant Sci. 2007;12:239-44.
95. Chini A, Fonseca S, Chico JM, Fernandez-Calvo P, Solano R. The ZIM domain mediates homo- and heteromeric interactions between Arabidopsis JAZ proteins. Plant J. 2009;59:77-87.
96. Ismail A, Riemann M, Nick P. The jasmonate pathway mediates salt tolerance in grapevines. J Exp Bot. 2012;63:2127-39.

97. Jumali SS, Said IM, Ismail I, Zainal Z. Genes induced by high concentration of salicylic acid in *Mitragyna speciosa*. Aus J Crop Sci. 2011;5:296-303.
98. Zhang S, Klessig D. Salicylic acid activates a 48-kD MAP kinase in tobacco. Plant Cell. 1997; 9:809-24.
99. Xiong L, Yang Y. Disease resistance and abiotic stress tolerance in rice are inversely on some physiological parameters symptomatic for oxidative stress and mineral nutrition in maize (*Zea mays* L.) grown under salinity. J Plant Physiol. 2003;164:728-36.
100. Barba-Espin G, Clemente-Moreno MJ, Lvarez S, Garcia-Legaz MF, Hernandez JA, Diaz-Vivancos P. Salicylic acid negatively affects the response to salt stress in pea plants. Plant Biol. 2011;13:909-17.
101. Jung J, Park C. Auxin modulation of salt stress signaling in Arabidopsis seed germination. Plant Signal Behav. 2011;6:1198-1200.
102. Park J, Kim YS, Kim SG, Jung JH, Woo JC, Park CM. Integration of auxin and salt signals by the NAC transcription factor NTM2 during seed germination in Arabidopsis. Plant Physiol. 2011;156:537-49.
103. Egamberdieva D. Alleviation of salt stress by plant growth regulators and IAA producing bacteria in wheat. Acta Physiol Plant. 2009;31:861-64.
104. Tirkayi I. The role of auxin-signaling gene axr1 in salt stress and jasmonic acid inducible gene expression in *Arabidopsis thaliana*. J Cell Mol Bio. 2007;6:189-95.
105. Akbari G, Sanavy SA, Yousefzadeh S. Effect of auxin and salt stress (NaCl) on seed germination of wheat cultivars (*Triticum aestivum* L.). Pak J Biol Sci. 2007;10:2557-61.
106. Fang B, Yang LJ. Evidence that the auxin signaling pathway interacts with plant stress response. Acta Botanica Sinica. 2002;44:532-36.
107. Hisamatsu T, Koshioka M, Kubota S, Fujime Y, King RW, Mander LN. The role of gibberellin in the control of growth and flowering in *Matthiola incana*. Physiol Plantarium. 2000;109:97-105.
108. Hamayun M, Khan SA, Khan AL, Shin JH, Ahmad B, Shin DH, Lee IJ. Exogenous gibberellic acid reprograms soybean to higher growth and salt stress tolerance. J Agric Food Chem. 2010;58: 7226-32.
109. Alonso-Ramírez A, Rodriguez D, Reyes D, Jimenez JA, Nicolas G, Lopez-Climent M, Gomez- Cadenas A, Nicolas C. Evidence for a role of gibberellins in salicylic acid-modulated early plant responses to abiotic stress in Arabidopsis seeds. Plant Physiol. 2009; 150:1335-44.
110. Iqbal N, Nazar R, Khan MIR, Masood M, Khan N. Role of gibberellins in regulation of source–sink relations under optimal and limiting environmental conditions. Current Sci. 2011;100:998-1007.
111. Tuna AL, Kaya C, Dikilitas M, Higgs D. The combined effects of gibberellic acid and salinity on some antioxidant enzyme activities, plant growth parameters and nutritional status in maize plants. Environ Expt Bot. 2008;63:1-9.
112. Kaya C, Tuna AL, Yoka I. The role of plant hormones in plants under salinity stress. In: Ashraf M, Ozturk M, Arthur H, editors. Salinity and water stress: Improving crop efficiency. Springer: Netherland; 2009;45-50.
113. Mohammed AHMA. Physiological aspects of mungbean plant (*Vigna radiate* L. Wilczek) in response to salt stress and gibberellic acid treatment. Res J Agr Biol Sci. 2007;3:200-13.
114. Chakrabarti N, Mukharji S. Alleviation of NaCl stress by pretreatment of phytohormones in *Vigna radiata*. Biol Plant. 2003;46:589-94.
115. Nishiyama R , Le DT, Watanabe Y, Matsui A, Tanaka M, Seki M, et al. Transcriptome analyses of a Salt-Tolerant Cytokinin-Deficient Mutant Reveal Differential Regulation of salt stress response by cytokinin deficiency. PloS ONE. 2012;23:2169-83.

116. Vyroubalova S, Vaclavıkova K, Tureckova V, Novak O, Smehilova M, Hluska T, et al. Characterization of new maize genes putatively involved in cytokinin metabolism and their expression during osmotic stress in relation to cytokinin levels. Plant Physiol. 2009;151:433-47.
117. Wang J, Ding H, Zhang A, Ma F, Cao J, Jiang M. A novel mitogen-activated protein kinase gene in maize (*Zea mays*),*ZmMPK3*, is involved in response to diverse environmental cues. J Integrative Plant Bio. 2010;52:442-52.
118. Keskin BC, Sarikaya AT, Yuksel B, Memon AR. Abscisic acid regulated gene expression in bread wheat. Aust J Crop Sci. 2010;4:617-25.
119. Li S, Xu C, Yang Y, Xia G. Functional analysis of *TaDi19A*, a salt-responsive gene in wheat. Plant Cell Environ. 2010;33:117-29.
120. Peter- Poor, Irma T. Ethylene-regulated reactive oxygen species and nitric oxide under salt stress in tomato cell suspension culture. Acta Biol Szegediensis. 2011;55:143-46.
121. Chen T, Yang Q, Zhang X, Ding W, Gruber M. An alfalfa (*Medicago* sativa L.) ethylene response factor gene, *MsERF11*, enhances salt tolerance in transgenic Arabidopsis. Plant Cell Rep. 2012;31:1737-46.
122. Cao YR, Chen SY, Zhang JS. Ethylene signaling regulates salt stress response. Plant Signal Behav. 2008;3:761-63.
123. Zander M, La Camera S, Lamotte O, Metraux JP, Gatz C. *Arabidopsis thaliana* class-II TGA transcription factors are essential activators of jasmonic acid/ethylene-induced defense responses. Plant J. 2010;61:200-21.
124. Zhang L, Li Z, Quan R, Li G, Wang R, Huang R. An AP2 domain containing gene , *ESE1*, targeted by ethylene signaling component EIN3 is important for the salt tolerance in Arabidopsis. Plant Physiol. 2011;157:854-65.
125. Chuang H, Harnrak A, Chen Y, Hsu C. A harpin-induced ethylene-responsive factor regulates plant growth and responses to biotic and abiotic stresses. Biophysical Res Communic. 2010;402:410-20.
126. Seo YJ, Park JB, Cho YJ, Jung C, Seo HS, Park SK, Nahm BH, Song JT. Overexpression of the ethylene-responsive factor gene *BrERF4* from *Brassica rapa* increases tolerance to salt and drought in Arabidopsis. Plants Mol Cells. 2010;30:97-106.
127. Wang H, Liang X, Wan Q, Wang X, Bi Y. Ethylene and nitric oxide are involved in maintaining ion homeostasis in Arabidopsis callus under salt stress. Planta. 2009;230:293-307.
128. Achard P, Cheng H, Grauwe L, Decat J, Schoutteten H, Moritz T, Van Der Straeten D, Peng J, Harberd NP. Integration of plant responses to environmentally activated phytohormonal signals. Sci. 2006;311:91-4.
129. Wu L, Zhang Z, Zhang H, Wang XC, Huang R. Transcriptional modulation of ethylene response factor protein *JERF3* in the oxidative stress response enhances tolerance of tobacco seedlings to salt, drought, and freezing. Plant Physiol. 2008;148:1953-63.
130. Zhao L, Zhang F, Guo J, Yang Y, Li B, Zhang L. Nitric oxide functions as a signal in salt resistance in the calluses from two ecotypes of Reed. Plant Physiol. 2004;134:849-57.
131. Cao WH, Liu J, Zhou QY, Cao YR, Zheng SF, Du BX, Zhang JS, Chen SY. Expression of tobacco ethylene receptor NTHK1 alters plant responses to salt stress. Plant Cell Environ. 2006;29:210-09.
132. Kawano T, Muto S. Mechanism of peroxidase actions for salicylic acid induced generation of active oxygen species and an increase in cytosolic calcium in tobacco cell suspension culture. J Exp Bot. 2000;51:685-93.

133. Lei G, Shen M, Li Z-G, Zhang B, Duan K-X, Wang N et al. EIN2 regulates salt stress response and interacts with a MA3 domain-containing protein *ECIP1* in Arabidopsis. Plant Cell Environ. 2011;34:1678-92.
134. Pedranzani H, Racagni G, Alemano S, Miersch O, Ramirez I, Pena-Cortes H, Taleisnik E, Machado-Domenech E, Abdala G. Salt tolerant tomato plants show increased levels of jasmonic acid. Plant Growth Regul. 2003;41:149-58.
135. Kang DJ, Seo YJ, Lee JD, Ishii R, Kim KU, Shin DH, Park SK, Jang SW, Lee IJ . Jasmonic acid differentially affects growth, ion uptake and abscisic acid concentration in salt-tolerant and salt- sensitive rice cultivars. J Agron Crop Sci. 2005;191:273-82.
136. Moons A, Prinsen E, Bauw G, Montagu MV. Antagonistic effects of abscisic acid and jasmonates on salt stress-inducible transcripts in rice roots. The Plant Cell. 1997;9:2243-59.
137. Gould KS, Lamotte O, Klinguer A, Pugin A, Wendehenne D. Nitric oxide production in tobacco leaf cells: a generalized stress response. Plant Cell Environ. 2003;26:1851-62.
138. Kopyra M, Gwozdz EA. Nitric oxide stimulates seed germination and counteracts the inhibitory effect of heavy metal and salinity on root growth of *Lupinus luteus*. Plant Physiol Biochem. 2003;41:1011-17.
139. Leterrier M, Chaki M, Airaki M, Valderrama R, Palma JM, Barroso JB, Corpas FJ. Function of S-nitrosoglutathione reductase (GSNOR) in plant development and under biotic/abiotic stress. Plant Signal Behav. 2011;6:789-93.
140. Leterrier M, Valderrama R, Chaki M, Airaki M, Palma JM, Barroso JB, Corpas FJ. Function of nitric oxide under environmental stress conditions. In : Khan N, Nazar R, Iqbal N, Anjum N, editors. Phytohormones and abiotic stress tolerance in plants. Springer Heidelberg Dordrecht: London, New York; 2012;99-113.
141. Sheokand S, Bhankar V, Sawhney V. Ameliorative effect of exogenous nitric oxide on oxidative metabolism in NaCl treated chickpea plants. Braz J plant physiol. 2010;22:81-90.
142. Guo Y, Tian Z, Yan D, Zhang J, Qin P. Effects of nitric oxide on salt stress tolerance in *Kosteletzkya virginica*. Life Sci J. 2009;6:67-75.
143. Gemes K, Poor P, Horvath E, Kolbert Z, Szopko D, Szepesi A, Tari I. Cross-talk between salicylic acid and NaCl-generated reactive oxygen species and nitric oxide in tomato during acclimation to high salinity. Physiol Plant. 2011;142:179-92.
144. Zhang F, Wang Y, Yang Y, Wu H, Di W, Liu J. Involvement of hydrogen peroxide and nitric oxide in salt resistance in the calluses from *Populus euphratica*. Plant Cell Environ. 2007;30:775-85.
145. Hai-Hua R, Wen-Bao S, Kai-Li L, Lang-Lai X. Effect of exogenous NO donor on glutathione dependent antioxidative system in wheat seedling leaf under salt stress. Acta Agronomica Sinica. 2005;31:1144-49.
146. El-Tayeb MA. Response of barley grains to the interactive effect of salinity and salicylic acid. Plant Growth Regul. 2005;45:215-24.
147. Horvath E, Szalai G, Janda T. Induction of abiotic stress tolerance by salicylic acid signaling. J Plant Growth Regul. 2007;26:290-300.
148. He Y, Zhu ZJ. Exogenous salicylic acid alleviates NaCl toxicity and increases antioxidative enzyme activity in *Lycopersicon esculentum*. Biol Plant. 2008;52:792-95.
149. Rajjou L, Belghazi M, Huguet R, Robin C, Moreau A, Job C et al. Proteomic investigation of the effect of salicylic acid on Arabidopsis seed germination and establishment of early defense mechanisms. Plant Physiol. 2006;141:910-23.
150. Abreu ME, Munne-Bosch S. Salicylic acid deficiency in *NahG* transgenic lines and sid2mutants increases seed yield in the annual plant *Arabidopsis thaliana*. J Exp Bot. 2009;60:1261-71.

151. Lee S, Kim SG, Park CM. Salicylic acid promotes seed germination under high salinity by modulating antioxidant activity in Arabidopsis. New Phytol. 2010;188:626-37.
152. Huang H, Cao H, Niu Y, Dai S. Expression analysis of nudix hydrolase genes in *Chrysanthemum lavandulifolium*. Plant Mol Biol Rep. 2012;30:973-82.
153. Mhamdi A, Hager J, Chaouch S. Arabidopsis glutathione reductase 1 plays a crucial role in leaf responses to intracellular $H_2O_2$and in ensuring appropriate gene expression through both salicylic acid and jasmonic acid signaling pathways. Plant Physiol. 2010;153:1144-60.
154. Nikiforova V, Freitag J, Kempa S, Adamik M, Hesse H, Hoefgen R. Transcriptome analysis of sulphur depletion in *Arabidopsis thaliana*: interlacing of biosynthetic pathways provides response specificity. Plant J. 2003;33:633-50.
155. Guilfoyle TJ, Hagen G. Auxin response factors. Curr Opin Plant Biol. 2007;10:453-60.
156. Dan H, Yang G, Zheng ZL. A negative regulatory role for auxin in sulfate deficiency response in *Arabidopsis thaliana*. Plant Mol Biol. 2007;63:221-35.
157. Hirai MY, Saito K. Post-genomics approaches for the elucidation of plant adaptive mechanisms to sulphur deficiency. J Exp Bot. 2004;55:1871-79.
158. Maruyama-Nakashita A, Inoue E, Watanabe-Takahashi A, Yarnaya T, Takahashi H. Transcriptome profiling of sulfur-responsive genes in Arabidopsis reveals global effects of sulfur nutrition on multiple metabolic pathways. Plant Physiol. 2003;132:597-605.
159. Chen J-H, Jiang H-W, Hsieh E-J, Chen H-Y, Chein C-T, Hsieh H-L, et al. Drought and salt stress tolerance of an Arabidopsis glutathione-S-transferase U17 knockout mutant are attributed to the combined effect of glutathione and abscisic Acid. Plant Physiol. 2012;158:340-51.
160. Jiang HW, Liu MJ, Chen IC, Huang CH, Chao LY, Hsieh HL. A glutathione S-transferase regulated by light and hormones participates in the modulation of Arabidopsis seedling development. Plant Physiol. 2010;154:1646-58.
161. Huang P-M, Chen J-Y, Wang S-J. Tissue-specific regulation of rice molybdenum cofactor sulfurase gene in response to salt stress and ABA. Acta Physiol Plant. 2009;31:545-51.
162. Burstenbinder K, Rzewuski G, Wirtz M, Hell R, Sauter M. The role of methionine recycling for ethylene synthesis in Arabidopsis. Plant J. 2007;49:238-49.
163. Nikiforova VJ, Bielecka M, Gakière B, Krueger S, Rinder J, Kempa S. Effect of sulfur availability on the integrity of amino acid biosynthesis in plants. Amino Acids. 2006;30:173-83.
164. Masood A, Iqbal N, Khan NA. Role of ethylene in alleviation of cadmium-induced photosynthetic capacity inhibition by sulphur in mustard. Plant Cell Environ. 2012;35:524-33.
165. Masood A, Iqbal N, Khan MIR, Khan NA. The coordinated role of ethylene and glucose in sulfur-mediated protection of photosynthetic inhibition by cadmium. Plant Signal Behav. 2012;7:1-3.
166. Lu CW, Shao Y, Li L, Chen AJ, Xu WQ, Wu KJ. Overexpression of *SlERF1* tomato gene encoding an ERF-type transcription activator enhances salt tolerance. Russ J Plant Physiol. 2011;58:118-25.
167. Jost R, Altschmied L, Bloem E, Bogs J, Gershenzon J, Hahnel U, et al. Expression profiling of metabolic genes in response to methyl jasmonate reveals regulation of genes of primary and secondary sulfur-related pathways in *Arabidopsis thaliana*. Photosynth Res. 2005;86:491-508.
168. Maruyama-Nakashita A, Nakamura Y, Tohge T, Saito K, Takahashi H. Arabidopsis *SLIM1* is a central transcriptional regulator of plant sulfur response and metabolism. Plant Cell. 2006;18:3235-51.

169. Xiang C, Oliver DJ. Glutathione metabolic genes coordinately respond to heavy metals and jasmonic acid in Arabidopsis. Plant Cell. 1998;10:1539-50.
170. Chassot C, Buchala A, Schoonbeek HJ, Métraux JP, Lamotte A. Wounding of Arabidiopsis leaves causes a powerful but transient protection against Botrytis infection. Plant J. 2008;55:555-67.
171. Ndamukong I, Abdallat AA, Thurow C, Fode B, Zander M, Weigel R Gatz C. SA-inducible Arabidopsis glutaredoxin interacts with TGA factors and suppresses JA-responsive PDF1.2transcription. Plant J. 2007;50:128-39.
172. Mueller S, Hilbert B, Dueckershoff K, Roitsch T, Krischke M, Mueller MJ, Berger S General detoxification and stress responses are mediated by oxidized lipids through TGA transcription factors in Arabidopsis. Plant Cell. 2008;20:768-85.
173. Cano A, Artés F, Arnao MB, Sánchez-Bravo J, Acosta M. Inhibition of etiolated lupin hypocotyl growth and rooting by peroxides, ascorbate and glutathione. J Plant Physiol. 1996;147:721-28.
174. Tonon C, Terrile MC, Iglesias MJ, Lamattina L, Casalongue C. Extracellular ATP, nitric oxide and superoxide act coordinately to regulate hypocotyls growth in etiolated Arabidosis seedlings. J Plant Physiol. 2010;167:540-46.
175. Terrile MC, Paris R, Villalobos LIAC, Iglesias MJ, Lamattina L, Estelle M et al. Nitric oxide influences auxin signaling through S-nitrosylation of the Arabidopsis TRANSPORT INHIBITOR RESPONSE 1 auxin receptor. The Plant J. 2012;70:492-500.
176. Lombardo MC, Graziano M, Polacco J, Lamattina L. Nitric oxide functions as a positive regulator of root hair development. Plant Signal Behav. 2006;1:28-33.
177. Terrile MC, Tonon CV, Iglesias MJ, Lamattina L, Casalongue CA. Extracellular ATP and nitric oxide signaling pathways regulate redox-dependent responses associated to root hair growth in etiolated Arabidopsis seedlings. Plant Signal Behav. 2010;5:698-701.
178. Tada Y, Spoel SH, Pajerowska-Mukhtar K, Mou Z, Song J, Wang C, Zuo J, Dong X. Plant immunity requires conformational charges of *NPR1* via S-nitrosylation and thioredoxins. Sci. 2008;321:952-56.
179. Koornneef A, Leon-Reyes A, Ritsema T, Verhage A, Den Otter FC, Van Loon LC , Pieterse CMJ. Kinetics of salicylate-mediated suppression of jasmonate signaling reveal a role for redox modulation. Plant Physiol. 2008;147:1358-68.

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