



The key roles of salicylic acid and sulfur in plant salinity stress tolerance

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Abstract

The salinization of agriculture soils over the globe has become one of the most devastating stresses and is significantly limiting cultivated land area, and crop productivity and quality. It is very imperative to explore both salinity tolerance in plants and insights into approaches (and underlying mechanisms) for effectively controlling salinity impacts. To this end, the role of phytohormone salicylic acid (SA) and plant nutrient sulfur (S) in promoting salinity tolerance has been researched in isolated studies, and SA–S interaction results have been little discussed. Given this, taking into account recent literature on SA, S and soil salinity, this paper aimed to (i) overview of the major impacts of soil salinity on plant health; (ii) highlight the significance of SA and S in improving plant salinity tolerance; (iii) discuss the role and underlying mechanism of SA, S and their interaction in the modulation of plant growth and development under salinity stress; and also to (iv) appraise the discussed literature and enlighten the major prospects.

Keywords Salinity · Sulfur · Salicylic acid · Phytohormones · Salinity tolerance

Introduction

Salinity stress and plant health

The world agriculture is under serious threat due to the increasing human population, and reduction in the arable land (Shahbaz and Ashraf 2013). Additionally, abiotic stresses as a major contributing factor decrease productivity by more than 50%. One of the factors, salinity stress, is increasing rapidly and is becoming the main concern for reductions in crop productivity and quality (Shahbaz and Ashraf 2013). Notably, the increasing salinization of world cultivable lands at an annual rate of 10% has been estimated to be culminated into more than 50% of the arable land be salinized by the year 2050 (Jamil et al.

2011). The soil salinity may develop as natural or induced by human activity. The long-term natural accumulation of salts (including Cl^- of Na^+ , Ca^{2+} and Mg^{2+} and sometimes SO_4^{2-} and CO_3^{2-}) in the soil or surface water contributes to the primary or natural salinity. On the other hand, the disruption of the hydrologic balance of the soil between water applied (irrigation or rainfall) and water used by crops (transpiration) as a result of anthropogenic activities cause the secondary soil salinity (Munns 2005; Hasanuz-zaman et al. 2011). Soils are regarded as saline when the saturation extracts (ECe) in the root zone exhibits: electrical conductivity (EC) $> 4.0 \text{ dS m}^{-1}$ ($\approx 40 \text{ mM NaCl}$) at 25°C and 15% exchangeable Na^+ ion. Potential mechanisms underlying salinity impacts in plants include: (i) salinity-mediated impairments in growth and development via water stress; (ii) cytotoxicity due to excessive uptake of ions such as Na^+ and Cl^- ; (iii) impaired nutritional imbalance and metabolism of mineral nutrients; and (iv) oxidative stress due to physiological imbalance between oxidants and antioxidants (Isayenkov and Maathuis 2019). Halophytic group of plants can tolerate up to 1.0 M salt concentration, whereas most crop plants are glycophytes and exhibit significant variations in their tolerance to salinity levels (Srivastava et al. 2015). A salt concentration of the saturation extracts up to 10 g/l can be tolerated by

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the highly tolerant crops, whereas the moderately tolerant crops can withstand salt concentration up to 5.0 g/l. The sensitive crops cannot tolerate even 2.5 g/l (Shahbaz and Ashraf 2013). Contingent to the concentration and time of exposure of salt, plant genotypes, and environmental factors, salinity impact on plant growth, development, and physiological/biochemical processes greatly vary in plants (Hasanuzzaman et al. 2011).

Salinity impacts every aspect of growth and development of plants. Briefly, seed germination is the first growth stage of the plant's life cycle and is very salinity-sensitive, and often exhibits high mortality rates. Moreover, plant salt-tolerance at the germination stage has been considered critical for the successful growth of plants in saline conditions. Salinity impact on the germination has been reported in several crop plants including *Arabidopsis* (Xu et al. 2011), *Zea mays* (Carpici et al. 2010; Khodarahmpour et al. 2012), and *Brassica* spp. (Ulfat et al. 2007). The variation in salinity tolerance may occur within species, cultivar, or individual lines at their growth stage (Parihar et al. 2015). Any change in various components of photosynthesis can have profound effects on its overall status in plants under stress. Salinity stress severely impacts all the phases of photosynthesis (Ashraf and Harris 2013; Jahan et al. 2019, 2020; Sehar et al. 2019).

Salinity stress impacts reactive oxygen species (ROS) and the antioxidants-mediated metabolism in plants (Choudhury et al. 2013; Anjum et al. 2015; Sehar et al. 2019; Jahan et al. 2020). ROS such as H_2O_2 , $O_2^{\bullet-}$ and $\bullet OH$ are capable of degrading lipids, proteins, and other macromolecules leading to the cellular metabolic arrest. On the other hand, salinity stress can also differentially modulate the major components of the antioxidant defense system (Sehar et al. 2019; Jahan et al. 2020). In turn, the elevation in ROS-metabolizing enzymes and/or metabolites can help salinity-exposed plants to efficiently scavenge varied ROS and also minimize ROS-caused potential consequences. NaCl stress-induced elevation in the activity of catalase and ascorbate peroxidase minimized the toxic effects of salinity in a number of studies (Ren et al. 2018; Jahan et al. 2019; Sehar et al. 2019 (Fig. 1).

Elevation in soil salinity can impact the uptake and metabolism of several plant nutrients including Ca, K, N, P and S (Nazar et al. 2011; Syeed et al. 2011; Astolfi and Zuchi 2013; Khan et al. 2015). Salinity-acrued disruption in the acquisition of the majority of these nutrients may involve direct competition between ions at various transporters in the root plasma membrane (such as K^+ -selective ion channels) or by the decreased osmotic potential of solution reducing the mass flow of mineral nutrients in the root (Parihar et al. 2015).

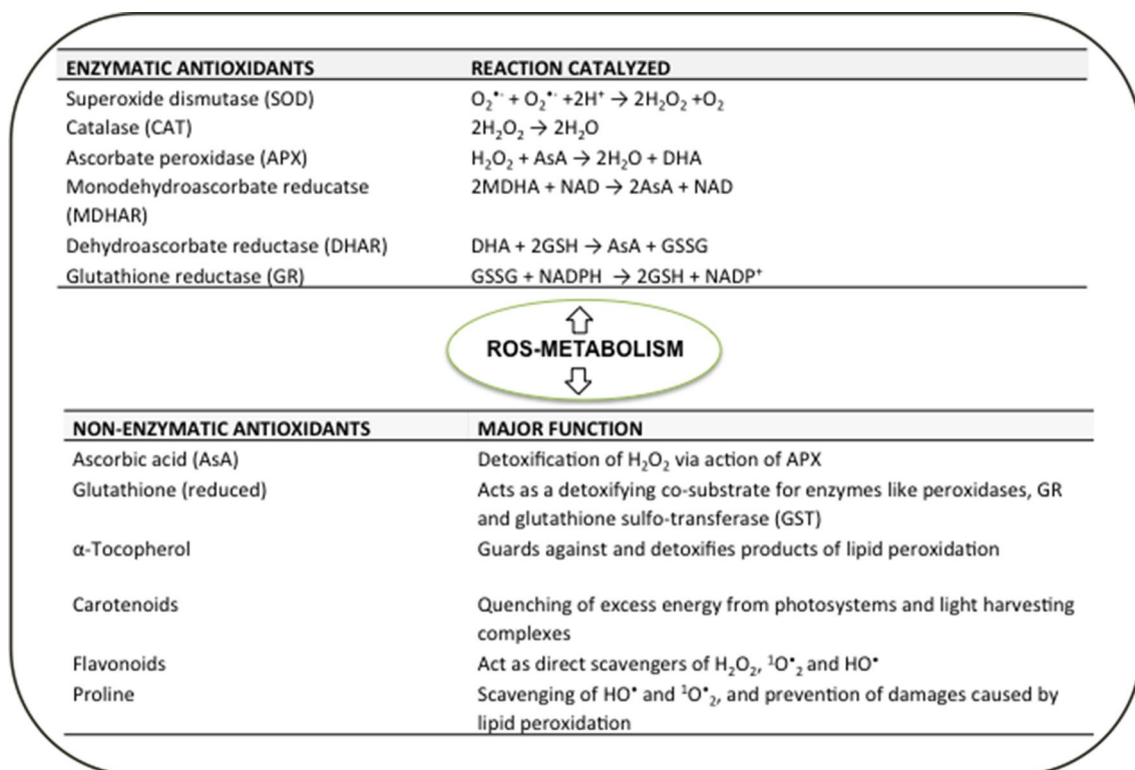


Fig. 1 Schematic representation of the major enzymatic antioxidants and non-enzymatic antioxidant involved in the metabolism of reactive oxygen species (ROS) in plants (modified after Das and Roychoudhury 2014)

Strategies for minimizing salinity stress impacts in plants

Reclamation of the salinity-affected soils has not always been feasible in minimizing the potential salinity impacts on plants/crops. Additionally, approaches to be adopted for controlling the salinity impacts on plants must be eco-friendly and sustainable. However, sustainable approaches (comprising microbial and molecular tools) to date adopted for the alleviation of salinity impact on plants are not a hundred percent feasible and cost-effective (Shokat and Großkinsky 2019). Hence, the adoption of approaches for modulating the plant's own physiological and metabolic strategies adopted for counteracting the salinity impact at the cellular and whole-plant levels can be promising.

Broadly, complex physiological traits, metabolic pathways, and molecular or gene networks are involved in the adaptation or tolerance of plants to salinity stress. However, the major mechanisms underlying the plant salinity tolerance are far from being completely understood. Hence, it is imperative to enlighten the major strategies to be adopted for the minimization of salinity stress impacts in plants. To this end, it has been widely reported that the strategies modulating many processes (including ion homeostasis, compatible solute accumulation, and osmotic adjustments and the regulation of cellular antioxidants) have significantly contributed to plant stress tolerance (Gupta and Huang 2014). To improve salinity tolerance, the majority of the aforesaid processes could be modulated in salinity-exposed plants by supplementing them with different exogenous bioregulators, such as osmoprotectants, phytohormones, signaling molecules, polyamines, antioxidants and various trace elements (Hasanuzzaman et al. 2013).

At the physiological level, osmotic adjustment is an adaptive mechanism involved in salinity tolerance. Osmolytes regulate osmotic adjustment and safeguard the proteins and other cell membranes against various stress factors on cellular metabolism (Sharma et al. 2019). Salinity-exposed plants were reported to exhibit the biosynthesis of osmoprotectants such as proline, glycine betaine, trehalose, sorbitol, glucose, and ectoine, where these molecules were argued to significantly contribute in hyperosmotic stress tolerance generated from salt stress (Hasanuzzaman et al. 2013). Compatible solutes have also been reported to mitigate the damaging effects of salt stress mainly by reducing the impact of stress-induced ROS (Cuin and Shabala 2008). Nitric oxide (NO) is a gaseous, free radical, and redox-signaling molecule with diverse functions, and it has been reported to affect plant responses to various stress factors including soil salinity (Sehar et al. 2019; Jahan et al. 2020). In salt-affected plants, NO can significantly improve the seed vigor and germination, scavenge ROS, alleviate oxidative damage, improve the antioxidant defense mechanism, plant growth, ionic balance

($K^+ : Na^+$, $Mg^{2+} : Na^+$, and $Ca^{2+} : Na^+$ ratios), water content, and chlorophyll content, and also increase chlorophyll a fluorescence curves (Ahmad et al. 2016; Sehar et al. 2019; Jahan et al. 2020). Another signaling molecule and non-proteino-genic amino acid β -aminobutyric acid was also reported to minimize salinity impacts in *Brassica napus* (Al-Mahmud et al. 2020). Phytohormones have long been considered as essential endogenous molecules involved in regulating plant development and tolerance or susceptibility of diverse stresses, including salinity (Ryu and Cho 2015). The list of phytohormones involved in salinity tolerance includes abscisic acid (ABA) (Ren et al. 2018), cytokinins (CK) (Wang et al. 2015), BRs (Ahanger et al. 2020), methyl jasmonate (MeJA) (Ryu and Cho 2015), gibberellin (GA) and ethylene (Khan et al. 2012), salicylic acid (SA) (Palma et al. 2013; Khan et al. 2015). On the other, minerals such as S (Nazar et al. 2011; Astolfi and Zuchi 2013), N (Iqbal et al. 2015; Singh et al. 2016), P (Fahad et al. 2016), Si (Coskun et al. 2016), Ca (Parvin et al. 2015), and many more are used for the salinity stress-alleviation in plants.

Prominence of salicylic acid and sulfur in stress acclimation

Salicylic acid has been widely reported to protect plants against abiotic stresses since it regulates important plant physiological processes including photosynthesis, nitrogen metabolism, proline (Pro) metabolism, glycine betaine production, control of antioxidant defense system, and plant–water relations (Khan et al. 2015). Additionally, SA can also induce defense-related genes and stress resistance in biotic stressed plants (Wani et al. 2016). A plethora of studies has confirmed the role of SA in plant tolerance to varied abiotic stresses including metals/metalloids (Khan et al. 2015; Zhang et al. 2015), salinity (Iqbal et al. 2014), ozone (Tamaoki 2008), UV-B radiation (Mohammed and Tarpley 2009), drought (Nazar et al. 2015b) and temperature stress (Siboza et al. 2017). On the other hand, plant stress tolerance can also be achieved by maintaining the status of plant-mineral nutrients such as S (Nazar et al. 2011; Rais et al. 2013; Fatma et al. 2014; Anjum et al. 2015; Hussain et al. 2019; Jahan et al. 2020). Both organic and inorganic forms of S are present in soils. Elementary S or its different oxidation forms (sulfide, sulfate, thiosulfate, etc.) represent the inorganically bound S and contribute only 10–15% of total S. Organically bound S occurs in organic compounds namely amino acids, proteins, polypeptides, and others, and contributes about 75–90% of the total S. The content of S in soils varies widely. In humid climates, S concentration is typically around 0.02–2.0%, moorland soils may contain 1.0% and in marshland, S concentration can be as high as around 3.5%. Therefore, organic matter content, soil parent material, and the amount of S added via fertilizer amendments and

atmospheric deposition are responsible for the wide variations in the total S in soils (Scherer 2009). Notably, the role of the major components and end products of S assimilation has been widely reported in plant tolerance to major abiotic stresses including metals/metalloids (Anjum et al. 2008; Khan et al. 2009a; Masood et al. 2012; Asgher et al. 2014), salinity (Khan et al. 2009b; Fatma et al. 2014; Husain et al. 2020), and chilling (Kopriva et al. 2001). Notably, there occurs a very close link between SA and S in terms of their physiological functions in plants under stress. For example, the interaction-outcomes of SA and S significantly contributed to plant growth, metabolism and stress tolerance; a higher GR activity and elevated S/Cys-GSH content were reported with exogenous SA (Pál et al. 2014); SA was involved in increased cysteine and GSH level as a result of SA-mediated increased activity of ATP-S and serine acetyltransferase (SAT) activity (Nazar et al. 2011, 2015a). Despite these facts, information is scanty in the literature available on approaches minimally impacting the environment, and the potential individual and combined roles of SA and S in eliminating soil salinity impacts on plant health and productivity.

Given these in light of recent literature, this paper aimed first to present a picture of the role and underlying mechanism of SA and S in the modulation of the response of germination, growth, photosynthetic and growth characteristics, oxidative stress markers, and the major components of both antioxidant defense system and S assimilatory pathways to soil salinity. Secondly, this paper appraises the discussed literature and also enlightens major knowledge-gaps on the subject.

Salicylic acid in mitigation of salinity impacts

Salicylic acid signaling in salinity tolerance

Of the two main pathways for SA biosynthesis (shikimic acid pathway and malonic acid pathway), the shikimic acid pathway is mainly involved in the endogenous synthesis of SA in plants, where phenylalanine, an aromatic amino acid acts as a precursor (Khan et al. 2015). On the other, the phenylalanine-mediated pathway of SA biosynthesis involves phenylalanine ammonia-lyase (PAL) and cinnamate-4-hydroxylase as the key enzymes. PAL converts phenylalanine into trans-cinnamic acid by the elimination of ammonium from phenylalanine, whereas cinnamate-4-hydroxylase converts cinnamic acid into coumaric acid by the hydroxylation at the C₄ position of cinnamic acid. Eventually, the oxidation of the side chain of coumaric acid followed by hydroxylation leads to the synthesis of SA (Per et al. 2017).

Once synthesized, SA is being transported in and out of the cells, tissues and organs, where several transporters are involved. Particularly under pathogen infections, only the methylated form (MeSA), considered to be the long-distance signaling molecule travels in plant tissue locally as well as systemically. Among the various forms of SA, Researchers have identified SA induction-deficient (*sid1* and *sid2*) in two *Arabidopsis thaliana*. Later, *sid1* was identified to be allelic to ENHANCED DISEASE SUSCEPTIBILITY 5 (*EDS5*), a member of the multidrug and toxin extrusion (MATE) transporter family (reviewed by Maruri-López et al. 2019). The process of SA signaling is initiated when the cells, tissues or organs are under (biotic/abiotic) stress. In turn, the binding of SA to some specific receptors has to occur in order to induce defense signaling. SA methyl transferase 1 (SAMT1) and SA-binding protein 2 (SABP2) are the major SA-receptors and control the balance between SA and MeSA (Jayakannan et al. 2015). The list of major SABPs involved in SA signaling network includes SABP1-catalase, SABP2-MeSA Esterase, SABP3-β carbonic anhydrase, non-expressor of pathogenesis-related protein 1–4 (NPR1/2/3/4)-signaling proteins, glutathione S-transferase isoenzymes (GSTF2, GSTF8, GSTF10, GSTF11), thioredoxin-m1 (TRXm1), GH3-acyl acid amido synthetase (GH3.12/PBS3), and glyceraldehyde 3-phosphate dehydrogenase (GAPDH; GAPA-1, GAPA-2, GAPC-1, and GAPC-2 (reviewed by Pokotylo et al. 2019). Recognized as an endogenous natural signal molecule SA regulates physiological and biochemical processes and thereby regulates growth and development and is also involved in defense mechanisms (Gunes et al. 2007; Iqbal et al. 2014; Khan et al. 2015). Extensive reports are also available on SA signaling and SA-mediated control of important genes involved in salinity-exposed plants (Csiszár et al. 2014; Jayakannan et al. 2015). A summary of recent studies reported on the aspect has been given in Table 1. Salicylic acid receptor, NPR1 (non-expressor of PR protein 1) is argued as a master regulatory protein of SA-dependent defense responses by being a transcriptional co-activator of PR-gene expression (Jayakannan et al. 2015). NPR1-mediated SA signaling has been argued pivotal for controlling Na⁺ entry into roots and the subsequent long-distance transport into shoots; enhancing H⁺-ATPase activity in roots, and increasing K⁺ concentration in shoots during salt stress (reviewed by Jayakannan et al. 2015). In salinity-exposed *Triticum aestivum*, SA (0.5 mM) was reported to bring enhancements in the transcriptomic rate of antioxidant genes such as *DHAR*, *GR*, *GPX*₂, *MDHAR*, *GST1*, *GST2*, and *GS* (Li et al. 2013). Salicylic acid-mediated upregulation of *SIGSTZ2*, *SIGSTL3*, and *SIGSTF4* of *GST* gene family has also been reported (Csiszár et al. 2014). Earlier, SA-supply was reported to enhance the expression of salt stress-mediated responsive genes encoding sinapyl alcohol dehydrogenase, cinnamyl alcohol dehydrogenase, cytochrome P450,

Table 1 Recent studies on the role of salicylic acid (SA) in salinity stress-mitigation for major parameters related with growth, photosynthesis, oxidative stress and antioxidant metabolism

Plants	Salinity level(s)	SA level(s)	Parameter/s	Response (\pm)	References
Growth parameters					
<i>Fragaria</i>	50 mM NaCl	100 and 500 μ M SA	Root length and leaf (dry and fresh) weight	+	Samadi et al. (2019)
<i>Glycine max.</i>	4, 7, 10 dS m^{-1} NaCl	1.0 mM SA	Leaf water content, potassium and calcium ions and plant biomass	+	Farhangi-Abri and Ghassemi-Golezani (2018)
<i>Solanum lycopersicum</i>	125 mM NaCl	0.01 mM SA	Shoot and root dry weight, leaf weight	+	Gharbi et al. (2018)
<i>Solanum chilense</i>	125 mM NaCl	0.01 mM SA	Leaf and root dry weight	+	Gharbi et al. (2017)
<i>Oryza sativa</i>	100 mM NaCl	1.0 mM SA	Plant height, number of tillers, leaves number	+	Jini and Joseph (2017)
<i>Fragaria</i>	0 and 60 mM NaCl	0.1, 0.5, and 0.75 mM SA	Fresh and dry weight of shoot and roots	+	Faghieh et al. (2017)
<i>Pisum sativum</i>	0, 100 and 150 mM NaCl	1.0 mM SA	Plant height, shoot and root dry matter	+	Ahmad et al. (2017)
Photosynthetic parameters					
<i>Fragaria</i>	50 mM NaCl	100 and 500 μ M SA	PS II activity	+	Samadi et al. (2019)
<i>Zea mays</i>	75 mM NaCl	1.0 mM SA	Leaf gas exchange parameters	+	Tahjib-Ul-Arif et al. (2018)
<i>Vigna radiata</i>	50, 100, 150 mM NaCl stress	50 μ M SA	Contents of chlorophyll a and b, total chlorophyll and carotenoids	+	Farheen et al. (2018)
<i>Cucumis sativus</i>	0 and 30 mM $NaHCO_3$	0, 50, 75, 100, 125, 150, 175 and 200 μ M SA	PSII quantum yield, PSII efficiency, net photosynthesis and the contents of chlorophyll and carotenoids	+	Nie et al. (2018)
<i>Solanum lycopersicum</i>	125 mM NaCl	0.01 mM SA	Net photosynthesis and stomatal conductance	+	Gharbi et al. (2018)
<i>Dianthus superbus</i>	0.5 mM SA	0.5 mM SA	Content of chlorophyll a, b, total chlorophyll and carotenoids	+	Zheng et al. (2017)
<i>Lawsonia inermis</i>	0, 65 and 134 mM NaCl	40 and 80 μ M SA	Content of chlorophyll a, b and total chlorophyll	+	Farahbakhsh et al. (2017)
Oxidative stress markers and antioxidants-related parameters					
<i>Fragaria</i>	50 mM NaCl	100 and 500 μ M SA	Lipid peroxidation (MDA content)	-	Samadi et al. (2019)
<i>Hordeum vulgare</i>	150 mM NaCl	0.5 mM SA	Extent of membrane lipid peroxidation and the content of H_2O_2	-	Torun (2019)
<i>Egletes viscosa</i>	80 mM of NaCl	1.0 mM SA	Extent of membrane lipid peroxidation	-	Batista et al. (2019)
<i>Glycine max.</i>	100 mM NaCl	0.5 mM SA	Activity of peroxidase, polyphenol oxidase and CAT	+	Oraghi Ardebili et al. (2019)
<i>Oryza sativa</i>	100 mM NaCl	0.5 or 1.0 mM SA	Na^+ , lipid peroxidation level and electrolyte leakage	-	Kim et al. (2018)
<i>Brassica carinata</i>	50, 100 and 150 mM NaCl	0.5 mM SA	Contents of proline and TBARS	-	Husen et al. (2018)
<i>Nitraria tangutorum</i>	100 mM NaCl	0.5 and 1.0 mM SA	Extent of membrane lipid peroxidation and the content of H_2O_2	-	Yan et al. (2018)

Table 1 (continued)

Plants	Salinity level(s)	SA level(s)	Parameter/s	Response (±)	References
<i>Oryza sativa</i>	100 mM NaCl	0.5 and 1.0 mM SA	Activity of CAT, SOD, and APX	–	Kim et al. (2018)
<i>Nitraria tangutorum</i>	100–400 mM NaCl	0.5 and 1.0 mM SA	Content of H ₂ O ₂ , and TBARS	–	Yan et al. (2018)
<i>Zea mays</i>	75 mM NaCl	1.0 mM SA	Activity of CAT and APX; MDA content	+	Tahjib_UI_Arif et al. (2018)
<i>Lawsonia inermis</i>	65 and 134 mM NaCl	40 and 80 µM SA	Electrolyte leakage (%) and CAT activity	+	Farahbakhsh et al. (2017)

Symbols + and – indicate increase and decrease, respectively, in the respective rows

heat shock proteins, and chaperones (Jumali et al. 2011). Salicylic acid can also regulate the expression of *NahG* (a bacterial gene encoding SA hydroxylase) for the response to salt stress (Nie et al. 2015). Salicylic acid was also involved in the regulation of the transcript levels of the *GA3ox1* gene and contributed to improved seed germination under salinity stress (Lee et al. 2010). Additionally, SA has also been reported to regulate Nudix hydrolases genes and the expression levels of both *CINUDX1* and *CINUDX2* under salt stress (Huang et al. 2012). Salicylic acid-induced accumulation of K⁺, and soluble sugars but decrease in Ca⁺ in roots; enhanced synthesis of photosynthetic pigments, and maintained membrane integrity (El-Tayeb 2005); strong inhibition in Na⁺ and Cl⁻ accumulation and stimulation in accumulation of N, Mg, Fe, Mn, P and Cu (Gunes et al. 2007); and the influence of SA on cation uptake in plants, and eventual modulation of the ratio of Na⁺ to other cations (Eraslan et al. 2008) were also reported potentially involved in SA-mediated plant salinity tolerance. Salicylic acid can also improve plant salinity tolerance by restoring membrane potential and preventing salt-induced K⁺ loss via a GORK channel (Jayakannan et al. 2013).

Sulfur in mitigation of salinity impacts

Sulfur assimilation

Among the major plant nutrients, S is a macronutrient for the plant and has been a major constituent in a range of S-amino acids like cysteine and methionine (Met), and S-compounds such as GSH, homo-GSH, and PCs. The assimilatory pathway of S in plants mainly involves: (i) ATP sulfurylase (ATP-S)-mediated activation of sulfate to adenosine 5'-phosphosulfate (APS);(ii) APS reductase (APR)-mediated reduction of APS into sulfite; and (iii) the reduction of sulfite into sulfide, and its incorporation into cysteine (Cys), a direct precursor for the synthesis of GSH (Anjum et al. 2015) (Fig. 2).

Sulfur-mediated salinity tolerance

In several studies, the assimilation of the applied S yielded the cellular Cys and GSH contents as a result of increased activity of ATP-S and thereby improved overall growth (Hussain et al. 2019; Nazar et al. 2011; Fatma et al. 2014, 2016). The supplied S-mediated improvements in the gas exchange parameters and photosynthetic pigments were also argued as a major mechanism underlying S-induced increases in intrinsic water-use efficiency (WUE) and ribulose 1,5 bisphosphate carboxylase/oxygenase (Rubisco) activity (Astolfi and Zuchi 2013; Khan et al. 2014b; Hussain et al. 2019) (Table 2). In several instances, the supplied S-led increases in the cellular S-containing compounds (such as GSH, methionine, thioredoxins, vitamins, and coenzyme A) and GSH-associated antioxidant enzymes were reported to strengthen antioxidant defense system in salinity-exposed plants (Nazar et al. 2011, 2014b; Astolfi and Zuchi 2013; Fatma et al. 2013, 2014; Hussain et al. 2019) (Fig. 3). Notably, among S-compounds, GSH, h-GSH, and PCs are known for their involvement in plant tolerance to varied abiotic stresses. Cys is a major component of GSH, h-GSH, and PCs, whereas several key stress-metabolites such as ethylene, are controlled by Met through its first metabolite SAM (Anjum et al. 2015). Salinity has been reported to significantly increase the transcript levels of both ATP-S and APR genes in plants (Sharma et al. 2015). These authors also observed a higher expression of APR genes in *B. juncea* seedlings even in the absence of stress with the expression of genes of both APR and ATP-S, much higher in tolerant cultivar compared to sensitive one. Earlier, the occurrence of a complex signaling network in the regulation of APR was reported in salinity-exposed Arabidopsis roots (Koprivova et al. 2008). Active uptake of sulfate uptake at the root plasma membrane is facilitated by the Group 1 sulfate transporters (Smith et al. 1995). Studies have reported Sultr1;2 as the primary sulfate transporter expressed in the root, but Sultr1;1 exhibited very

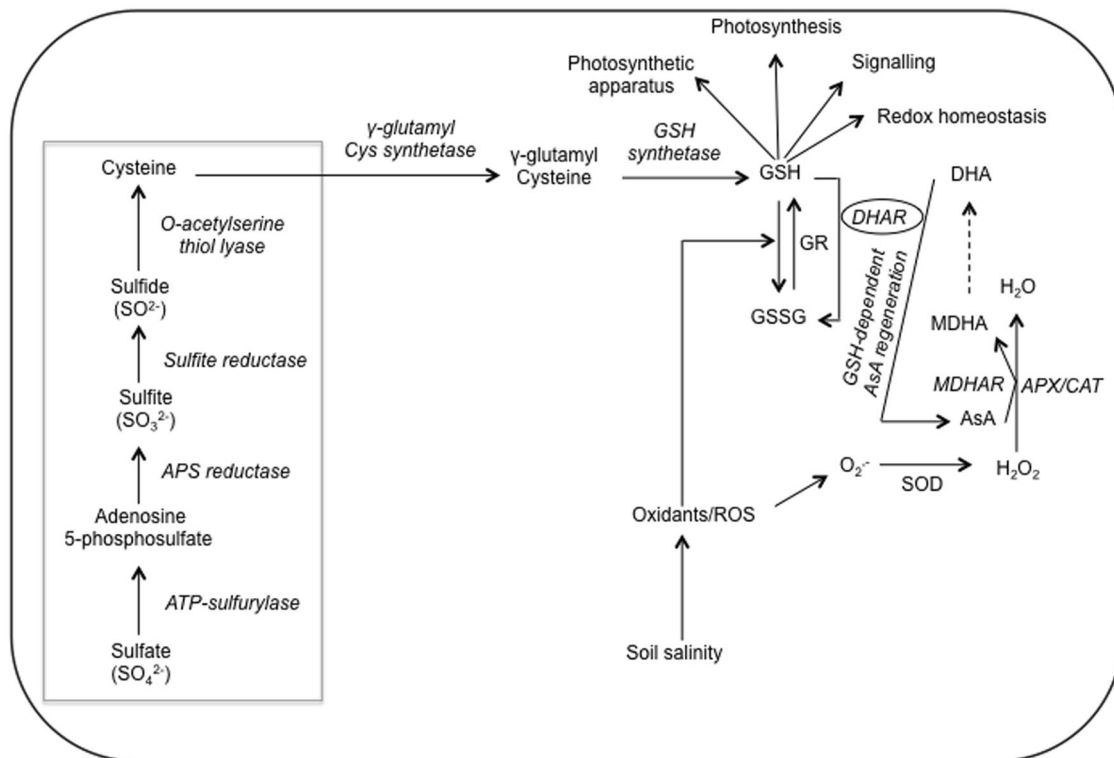


Fig. 2 Scheme representing the assimilation of sulfur (S), its involvement in the glutathione (GSH) synthesis, and GSH-mediated control of oxidants (reactive oxygen species, ROS) generated due to salinity in plants. GR, glutathione reductase; GSSH, oxidized glutathione;

AsA, reduced ascorbate; MDHA, monodehydroascorbate; DHAR, dehydroascorbate reductase; MDHAR, monodehydroascorbate reductase; APX, ascorbate peroxidase; CAT, catalase; SOD, superoxide dismutase. O₂⁻, superoxide; H₂O₂, hydrogen peroxide

low expression therein (Koralewska et al. 2008, 2009). The expression of APR in plants is regulated largely by reduced sulfur compounds (Koralewska et al. 2009; Davidian and Kopriva 2010). Notably, considered for a long time as a toxic by-product of cell metabolism, H₂S, used as an S-source, has been reported to contribute in regulating Na⁺/K⁺ balance (Mostofa et al. 2015; Jiang et al. 2019). H₂S-mediated maintenance of the Na⁺/K⁺ balance was evidenced to involve H₂S-induced regulation of the expression of plasma membrane H⁺-ATPase (PM H⁺-ATPase), salt overly sensitive 1 (SOS1), a plasma membrane Na⁺/H⁺ antiporter and SKOR, an outward rectifying K⁺ channel (Jiang et al. 2019). Notably, PM H⁺-ATPase is known to sustain an H⁺ gradient by promoting Na⁺ efflux and H⁺ influx to drive Na⁺/H⁺ antiport across the plasma membrane (Jiang et al. 2019). Earlier, H₂S-induced increase in Na⁺ extrusion and decrease in Na⁺ uptake and thereby plant salinity tolerance were argued to involve H₂S-mediated regulation of the membrane-bound translocation proteins of the SOS1 pathways (Deng et al. 2016). Additionally, H₂S-mediated regulation of the expression of SOS pathway genes was found to keep the balance of Na⁺ and K⁺ in the test plant (Christou et al. 2013).

Salicylic acid and S interaction with other phytohormones

In addition to interacting with plant nutrient S, SA has been reported to interact with several phytohormones, polyamines, nitric oxide, and also with other plant nutrients. In several reports, S co-coordinately worked with different phytohormones including auxins, gibberellins, cytokinins, abscisic acid, brassinosteroids, ethylene, nitric oxide, and salicylic acid in different plants (Pál et al. 2014; Khan et al. 2010, 2014a, b, 2015; Hasanuzzaman et al. 2018; Jahan et al. 2019). The results of the interaction of SA with nutrient S and other phytohormones significantly contributed to plant growth, metabolism, and stress tolerance (Hasanuzzaman et al. 2018). Exogenous SA can elevate S/Cys-GSH content, and also result in a higher GR activity (Pál et al. 2014). SA-mediated increase in GSH contents was argued as the result of the SA-mediated increase in activity of ATP-S and serine acetyltransferase (SAT), and the contents of S and Cys (Nazar et al. 2011, 2014a; Hussain et al. 2020). Notably, a sulfotransferase (*SOT12*) has been reported to regulate SA homeostasis via sulfation (Baek et al. 2010); and the S-nitrosylation was involved in SA signaling

Table 2 Recent studies on the role of sulfur (S) or its source in salinity stress-mitigation for major parameters related with growth, photosynthesis, oxidative stress and antioxidant metabolism

Plants	Salinity level(s)	S level(s)	Parameter/s	Response (+/-)	Reference
Growth parameters					
<i>Brassica rapa</i>	25, 50 and 100 mM NaCl	50 mM (S) sulfate	Dry matter and biomass	+	Reich et al. (2017)
<i>Zea mays</i>	0 and 90 mM NaCl	S-containing compounds FeSO ₄ (10 mM), LiSO ₄ (10 mM), cysteine (20 mM) and mixture (in 1:1:2 ratio); foliar spray	Root and shoot biomass, and length of root and shoot	+	Perveen et al. (2018)
<i>Lactuca sativa</i>	0 and 40 mM NaCl	0.0, 1.5 and 3.0 g L ⁻¹ ; foliar fertilization	Root growth and fresh mass of root	+	de Souza Freitas et al. (2019)
<i>Helianthus annuus</i>	0 and 100 mM NaCl	80 mg S kg ⁻¹ soil	Root fresh weight, stem girth, and total fresh weight of plant	+	Aziz et al. (2019)
<i>Capsicum</i> sp.	Salinity (5 dSm ⁻¹ EC)	5 or 10 g S L ⁻¹	Root and shoot length, and leaf area	+	Mukhtar et al. (2016)
<i>Pisum sativum</i>	Salinity (EC=8.5 dS m ⁻¹)	500 kg elemental S ha ⁻¹	Shoot lengths, the number of branches per plant, leaf area per plant, and shoot dry weight per plant	+	Osman and Rady (2012)
Photosynthetic parameters					
<i>Vigna radiata</i>	50 mM NaCl	1.0 and 2.0 mM SO ₄ ²⁻	Net photosynthetic rate, intercellular CO ₂ , stomatal conductance, intrinsic water-use efficiency and Rubisco activity	+	Hussain et al. (2019)
<i>Vigna radiata</i>	50 mM NaCl	2.0 mM SO ₄ ²⁻	Net photosynthetic rate, intercellular CO ₂ , stomatal conductance	+	Hussain et al. (2020)
<i>Lactuca sativa</i>	0 and 40 mM NaCl	0.0, 1.5 and 3.0 g L ⁻¹ ; foliar fertilization	Stomatal conductance and liquid photosynthesis	+	de Souza Freitas et al. (2019)
<i>Helianthus annuus</i>	0 and 100 mM NaCl	80 mg S kg ⁻¹ soil	Net photosynthetic rate	+	Aziz et al. (2019)
<i>Capsicum</i> sp.	Salinity (5 dSm ⁻¹ EC)	5 or 10 g S L ⁻¹	Net photosynthetic rate and stomatal conductance	+	Mukhtar et al. (2016)
Oxidative stress markers and antioxidants-related parameters					
<i>Vigna radiata</i>	50 mM NaCl	1.0 and 2.0 mM SO ₄ ²⁻	Extent of membrane lipid peroxidation and the content of H ₂ O ₂	-	Hussain et al. (2019)
<i>Oryza sativa</i>	150 mM NaCl	H ₂ S supplying 0, 25, 50, 100, and 200 μM NaHS	Extent of membrane lipid peroxidation and the content of H ₂ O ₂	-	Mostofa et al. (2015)
<i>Vigna radiata</i>	50 mM NaCl	1.0 and 2.0 mM SO ₄ ²⁻	GSH content and activity of SOD, APX and GR	+	Hussain et al. (2019)
<i>Vigna radiata</i>	50 mM NaCl	2.0 mM SO ₄ ²⁻	GSH content and the activity of APX and GR	+	Hussain et al. (2020)
<i>Zea mays</i>	0 and 90 mM NaCl	S-containing compounds FeSO ₄ (10 mM), LiSO ₄ (10 mM), cysteine (20 mM) and mixture (in 1:1:2 ratio); foliar spray	Total soluble sugars, ascorbic acid contents and total phenolics	+	Perveen et al. (2018)

Table 2 (continued)

Plants	Salinity level(s)	S level(s)	Parameter/s	Response (+/-)	Reference
<i>Zea mays</i>	100 mM NaCl	H ₂ S (0.6 mM NaHS)	Activity of APX, GR, DHAR and MDHAR, and ratio of GSH/GSSG	+	Shan et al. (2014)
<i>Lactuca sativa</i>	0 and 40 mM NaCl	0.0, 1.5 and 3.0 g L ⁻¹ ; foliar fertilization	SOD and CAT activity	+	de Souza Freitas et al. (2019)
<i>Helianthus annuus</i>	0 and 100 mM NaCl	80 mg S kg ⁻¹ soil	Electrolyte leakage	-	Aziz et al. (2019)

Symbols + and - indicate increase and decrease, respectively, in the respective rows

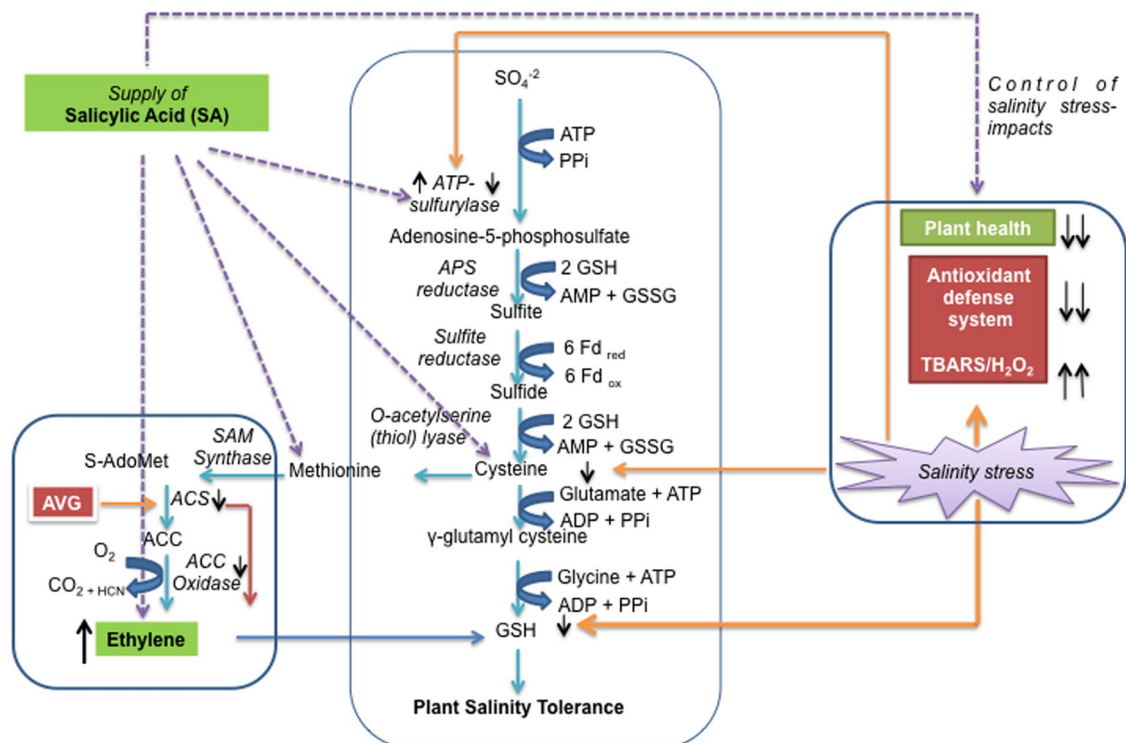


Fig. 3 Schematic representation of the potential mechanisms underlying the role of salicylic acid (SA), sulfur (S), and the result of the interaction between SA, S, and gaseous phytohormone ethylene in salinity impact-mitigation in plants. AVG, 2-aminoethoxyvinylglycine (ethylene biosynthesis inhibitor); ACC, 1-aminocyclopropane-1-car-

boxylate (ethylene precursor); ACS, 1-aminocyclopropane-1-carboxylic acid synthase; S-AdoMet, S-adenosyl methionine (ethylene production-precursor); APS, adenosine 5'-phosphosulfate; TBARS, thiobarbituric acid reactive substances; GSH, reduced glutathione

(Mikkelsen et al. 2003). SA-induced enhancement in the N and S assimilation hence inducing salinity tolerance in plants were reported to involve SA-mediated upregulation of the activity of enzymatic and non-enzymatic antioxidant systems (Nazar et al. 2011). The application of SA accelerated the uptake of P, N, K, Ca, Mg, and efflux of Na⁺ ions, and thereby increased the growth of salt-stressed *Cucumis sativus* and protected this crop against salinity impacts (Yildirim et al. 2008). In another instance, exogenously applied SA (0.5 mM) improved the growth, yield, and gas exchange in salt-stressed *Z. mays* by regulating the high ratio of K⁺/Na⁺

and Ca⁺/Na⁺ (Tufail et al. 2013). SA-mediated reversal of the salt-mediated alteration in the contents of Na, K, Ca, and Mg content was found in *T. aestivum* (Al-Hakimi and Hamada 2001). In combination with selenium, SA was found to reduce the temperature-accrued increased ROS by enhancing antioxidant metabolism and significantly reducing Na⁺/K⁺ ratio in NaCl exposed plants (Abdel-Salam 2016). SA-mediated reduction in the concentration of K and P was also reported in the shoot and root of salinity stressed *Z. mays* (Gunes et al. 2007). However, SA-supply was also reported to inhibit K⁺ uptake and accelerate Na⁺ in *S. lycopersicum*

supplied with SA (Szepesi et al. 2009). Yoshida and Noguchi (2009) found that SA improved the S uptake and regulated GSH biosynthesis during ozone stress in *Arabidopsis*.

The gaseous hormone ethylene has been reported to exhibit myriad roles in plants and modulation of growth and photosynthesis phenomena under optimal as well as stressful conditions (Khan and Khan 2014). Ethylene can also control photosynthesis through regulating stomatal movement and thereby allowing more influx of CO₂ for carboxylation under optimal and stressful environments (Iqbal et al. 2011, 2012; Masood et al. 2012; Khan et al. 2013). In another instance, ethylene-supply was reported to increase the stomatal aperture and thereby increased the diffusion rate of CO₂ from the atmosphere to the intercellular spaces (Acharya and Assmann 2009). There occurs a close relation between SA and 1-aminocyclopropane-1-carboxylic acid synthase (ACS) under stressful conditions, where SA can inhibit ethylene biosynthesis by restricting the conversion of 1-aminocyclopropane-1-carboxylate to ethylene, and protect plants against stress impacts (Khan et al. 2012, 2015). A close relation also exists between S, ethylene, and SA, where S is known to influence ethylene biosynthesis through SAM, ethylene production-precursor; and SA has been reported to inhibit ethylene (Masood et al. 2012; Khan et al. 2014a, b; Nazar et al. 2015b). The use of 2-aminoethoxyvinyl glycine (AVG), ethylene biosynthesis inhibitor) in the experiment blocked ethylene synthesis; however, it produced similar effects to SA and SA-analog, INA, on the contents of S-containing compounds (Hussain et al. 2019; Khan et al. 2014a, b). Also, AVG- and SA-mediated inhibition in the activity of ACS was reported in earlier studies (Khan et al. 2012, 2015). Thus, the interplay between SO₄²⁻, SA and ethylene can occur which may play a major role in the modulation of salinity-exposed plants supplied with nutrients such as S and/or phytohormone such as SA (Fig. 3).

Appraisal and prospects

The literature reviewed herein evidenced that soil-salinization is a major threat to agriculture. It has been the major stress factor for severely impacting crop health and reducing yield. There occurs a host of approaches for mitigating salinity stress impacts in plants. The strategy of using plant nutrient S and phytohormone SA has emerged as a potential approach for modulating several processes including ion homeostasis, compatible solute accumulation, and osmotic adjustments and the regulation of cellular antioxidants and eventually contributing to plant stress tolerance. It is noteworthy to mention here that through involvement in S-containing compounds, such as GSH and SAM, S contributes to salinity tolerance via directly or indirectly. On the other hand, the appraisal of the literature related to SA, it is suggested that exogenous SA could ameliorate the

salinity-toxicity symptoms in plants by improving photosynthetic capacity, enhanced antioxidant protection through modulating antioxidant defense system components, ROS-metabolism, and increasing accumulation of soluble carbohydrates. The role of S (or its source) is very clear in the regulation of Na⁺/K⁺ balance, the expression of plasma membrane H⁺ ATPase, SOS1, and SKOR in salinity stressed plants. However, the mechanism underlying the role of SA in the maintenance of ionic homeostasis under salinity stress is poorly understood (Jayakannan et al. 2015). To this end, on the one hand, the supplied SA decreased K⁺ and P in shoot and root tissues of salinity-exposed maize (Gunes et al. 2007) and barley shoots (El-Tayeb 2005). On the other hand, SA-supply failed to affect Na⁺ and Cl⁻ concentrations in salinized spinach roots and shoots (Eraslan et al. 2008); and also, SA-application inhibited K⁺ uptake and increased Na⁺ uptake in tomato plants (Szepesi et al. 2009). Additionally, the use of SA or S in salinity-exposed plants has been done either in isolated studies or SA and S have been cross-talked without convincing outcomes in context with plant salinity tolerance. The exploitation of S and SA as a stress management tool could be a subject of interest as this mineral nutrient and phytohormone combination can impart tolerance to many crops against the salinity. It is very imperative to unravel the insights into the major or minor regulatory point in S assimilation; SA-mediated regulated processes and the potential involvement of other phytohormones (such as ethylene) in SA + S-mediated salinity tolerance.

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Compliance with ethical standards

Conflict of interest There is no conflict of interest.

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