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SULFUR: A MACRONUTRIENT HAVING POTENTIAL TO IMPROVE SALINITY TOLERANCE IN PLANTS

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Abstract

Salinity causes disturbance in osmotic potential, imbalance in nutritional composition, and reduction in photosynthesis that reduces whole-plant growth and development. Amongst different strategies to overcome salt-induced toxicity, external application of mineral nutrients is a cost-effective and smart method. Sulfur (S) has substantial significance in relieving the toxic impacts of salt stress by increasing plant nutrients, water uptake, protein contents, and plant productivity. It is an essential constituent of different coenzymes, vitamins, and plant hormones. Various S metabolites are involved in developing salt tolerance by modulating various physiological and biochemical processes in plants. In the case of saline conditions, S helps in ionic homeostasis, optimizing water stress, regulation of mineral uptake, protection of photosynthetic apparatus, activating antioxidant machinery, reduction of electrolytic leakage and membrane stabilization. This review focuses on the significance of S in improving salt tolerance potential of plants by modulating various growth, physiological and biochemical processes. Moreover, the significance of various S metabolites and S salts with respect to salt tolerance has also been described.

Key words: Assimilation, Fertilizers, Metabolites, Salinity, Sulfur.

Introduction

In terms of biological requirement, S ranks fourth after nitrogen, potassium, and phosphorus. Sulfur performs many biological roles in plants. It is an important constituent of a number of amino acids (cysteine, methionine, S-glycosides and thiamine), oligopeptides (glutathione and phytochelatins), thioredoxin, sulfolipids, glycolipids, vitamins, and cofactors (biotin, thiamine, coenzyme A (CoA), and S-adenosyl-Methione) (Leustek, 2000). Combined with some macronutrients (*i.e.*, nitrogen, phosphorous, potassium, and calcium) and micronutrients (*i.e.*, zinc, manganese, iron, and silicon), S has a significant contribution in stopping the uptake and deposition of metals in plants (Sarwar *et al*., 2010). The photosynthetic efficiency of plants also improves due to the role of S in the formation of chlorophyll (Jamal *et al*., 2006). Besides being an important constituent of plant nutrition, it is a part of Fe-S proteins called ferredoxin, which transport electrons in the light reaction of photosynthesis. Biological nitrogen fixation, nodulation, activity of PEP carboxylase and concentration of proteins in leguminous crops has been reported to increase by exogenous application of S (Sahota, 2006). Therefore, S-containing compounds are very important in maintaining the growth and production quality of food crops (Perveen *et al*., 2018).

Soil and water salinity occurs when concentrations of dissolved solutes exceed a critical limit. The electrical conductivity (ECe) value of normal soil is lower than 2 d Sm^{-1}, while soil containing higher salinity (ECe = 4 d Sm^{-1}), is known as salt-affected (Weisany *et al*., 2012). According to an estimate, 954 million ha soils are affected by salinity worldwide, resulting in a 10-25% decrease in crop productivity (Shahid *et al*., 2018). Salinity causes nutritional imbalance, buildup of reactive oxygen species, and ion toxicity that disturbs various physiological, biochemical, and anatomical mechanisms of plants (Riffat & Ahmad, 2020b). Therefore, effective methods are needed to combat the problem of salt stress.

Inorganic nutrients have a significant role in reducing salt toxicity. Sulfur is a macronutrient with necessary roles in plant health and vigor under optimal as well as stressful environment. Sulfur application improves various biochemical processes in plants that trigger the activation of various genes and metabolites to combat salt stress (Shalaby, 2018; Saad-Allah & Ragab, 2020). Moreover, S alleviates the nutritional imbalance created by salinity and helps in improving crop growth and development and, ultimately plant yield (Riffat & Ahmad, 2018b; Riffat, 2018).

In view of the above aspects, the present review focuses a detailed overlook into various properties of S in combating salt stress, the efficiency of various S fertilizers in improving crop growth in salinity stress conditions, and roles of various S metabolites having a key contribution in counteracting salt toxicity in plants.

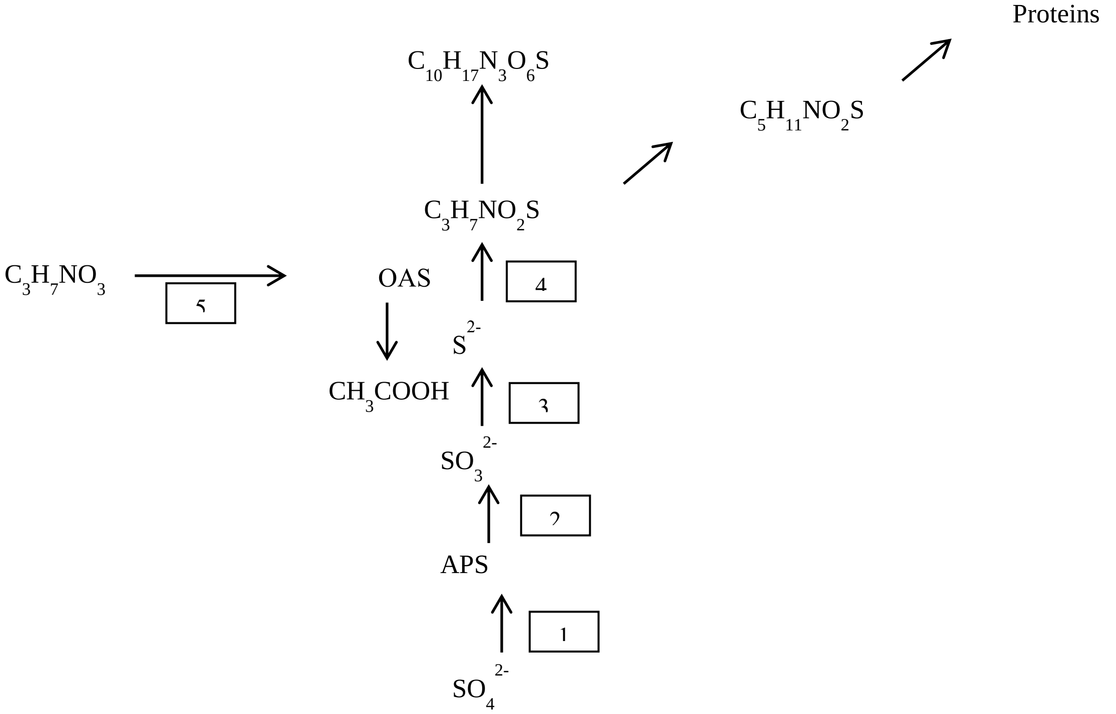
Sulfur uptake, transport and assimilation in plants: Sulfur is taken up by the plants in the form sulfate (SO_4^{2-}) ions via root hairs (Cacco *et al*., 1980), with the help of H^+/SO_4^{2-} co-transporter (Leusteck & Saito, 1999). The inflow of SO_4^{2-} occurs at pH = 4 which reduces by reducing pH. A high SO_4^{2-} uptake takes place from root apex. Bowen and Rovira (1971) found that a high uptake of S was observed in first 5 cm of root apex. The pathway of SO_4^{2-} uptake firstly involves root plasma membrane, then goes to vascular bundle in the xylem vessels and finally transported to shoot through transpiration stream. It is an energy dependant process which is mediated by a proton/sulfate co-transport which takes energy generated by ATPase (Clarkson *et al*., 1993).

Sulfate is transported from root to shoot with the help of various tans-membrane systems and long distance pathways in the xylem. The SO_4^{2-} loaded in xylem interacts with the water in the vertical axis. The transpiration stream performs as the motive force for the transport of SO_4^{2-} to the leaves, and then it is loaded to the mesophyll cell (Rennenberg *et al*., 1979). Sulfur present in phloem sap is reached in various plant organs (Zhao *et al*., 1999). Upon unloading into shoot, SO_4^{2-} is compartmentalized in the vacuole for maintaining SO_4^{2-} balance in cytoplasm.

Sulfate is reduced inside the plant body to various other S metabolites. Sulfate absorbed by roots is transported to shoot and converted to adenosine 5'-phosphosulfate (APS) by using ATP sulfurylase. Then APS is converted to sulfite by using glutathione as a reducing agent mediated by an enzyme APS reductase (Saito, 2003; Kaufmann & Sauter, 2019). Sulfite is then converted to sulfide using ferredoxin as a reducing agent and catalyzed by sulfite reductase enzyme. The sulfide so formed is converted to cysteine by O-acetylserine (thiol) lyase using O-acetylserine as substrate. O-acetylserine is formed by serine acetyltransferase. Upon formation of cysteine, various other S metabolites are prepared as their synthesis is an important direct-coupling stage of SO_4^{2-} assimilation in plants. The leftover SO_4^{2-} is transported to the plant vacuole (Hell, 2003; Maruyama-Nakashita, 2017; Chan *et al*., 2019; Li *et al*., 2020). The pathway of S assimilation is shown in (Fig. 1).

Role of sulfur in salt tolerance of plants

Improvement in soil properties to endure salt stress: Sulfur is very efficient and helpful in lowering salinity and alkaline stress by improving soil permeability, reducing soil pH, and lowering the loss of bicarbonates from irrigation water. Ali & Asalm (2005) proposed that exogenous application of S as sulfuric acid at 50 L ha^{-1} reduced soil pH that raised the wheat yield three times compared to control. Mohamed *et al*., (2019) evaluated that S application in saline conditions, reduced electrical conductivity, soil pH, and sodium absorption ratio and significantly improved nitrogen, phosphorous and potassium nutrient.



Abbreviations: SO_4^{2-} = Sulfate; APS = Adenosine 5'-phosphosulfate; SO_3^{2-} = Sulfite; S^{2-} = Sulfide; $C_3H_7NO_2S$ = Cystein; $C_5H_{11}NO_2S$ = Methionine; $C_{10}H_{17}N_3O_6S$ = Glutathione; $C_3H_7NO_3$= Serine; OAS = O-acetylserine; CH_3COOH = Acetate; 1 = ATPS; 2 = APS reductase; 3 = SO_3^{2-} reductase; 4 = O-acetylserine (thiol) lyase; 5 = Serine acetyl transferase

Fig. 1. Mechanism of sulfur assimilation in plants.

Improvement in plant growth and development: Sulfur has significant contribution in improving plant vigor to endure harsh conditions of salt stress. Earlier studies revealed that cysteine and glutathione produced during S assimilation causes rise in ATP-S activity which increases plant growth (Nazar *et al*., 2011; Fatma *et al*., 2014, 2016; Hussain *et al*., 2019). Reich *et al*., (2017) found that application of 50 mM SO_4^{2-} improved dry weight and plant biomass of *Brassica rapa* plants in saline environment. Ali *et al*., (2008) reported that the application of S to the rooting zone of wheat significantly improved the salt tolerance level and improved fresh and dry biomass of wheat cultivars. Parveen *et al*., (2018) evaluated that application of 10 mM $FeSO_4$, 10 mM $LiSO_4$ and 20 mM cysteine improved length of root and biomass of maize plants under salt stress conditions. Anjum *et al*., (2012) observed that application of nitrogen and S played a significant contribution in growth and development and ultimately productive capacity of *Oleiferous brassicas* cultivar through sulfur-nitrogen intervened preparation of antioxidants. de Souza Freitas *et al*., (2019) found that by applying S at the rate of 1.5 and 3.0 g L^{-1} under salinity, improved fresh weight of root and shoot in *Lactuca sativa*. Nakajima *et al*., (2019) stated that S has a pronounced contribution in growth and development of plants being a constituent of various amino acids and proteins. Aziz *et al*., (2019) while working on S effects under saline conditions found that application of 80 mg kg^{-1} S improved root and shoot fresh weight of *Helianthus annuus* plants. Mukhtar *et al*., (2016) evaluated that application of 5 or 10 g L^{-1} S increased length of shoot and root and leaf area of *Capsicum* spp. subjected to salinity. Osman & Rady (2012) applied 500 kg elemental S to salt stressed *Pisum sativum* plants and found that application of S increased shoot length, leaf area, and shoot dry weight. In a previous study it was demonstrated that application of salted water showed a significant decrease in all growth parameters in *Dalbergia sissoo*, while application of S significantly increased these parameters under irrigation with normal or saline water up to salt level of 4 g/L (Azza *et al*., 2006). Hence, application of S has significant contribution in improving overall plant growth under saline environment.

Improvement in physiochemical properties and productive capacity of plants: Sulfur improves the salt tolerance of plants by regulating various enzymes involved in S assimilation (Fig. 1). It is predictable that enzyme modulation that is involved in S metabolism in plants; can assist in reducing the toxic effects of salt stress through the contribution of its metabolites in a wide range of chemical reactions in plants; since many of them has been shown to be related to antioxidant machinery in plants in saline conditions (Riffat & Ahmad, 2020a). One possible reason of improving overall plant growth is that S is directly used in the synthesis of chlorophyll, proteins, vitamins, and glutathione that induce tolerance in plants against salinity. Appropriate S concentration normalizes chlorophyll contents, protein pool, and electron transport pathway and increases the activity of enzymes involved in photosynthesis. It is also involved in redox reactions and helps to stabilize proteins because it forms disulphide bonds (Spadaro *et al*., 2010; Riffat & Ahmad, 2016). Earlier studies revealed that application of S developed salt tolerance in a variety of plants. Hussain *et al*., (2020) found that application of 1 and 2 mM SO_4^{2-} to salt stressed plants improved net photosynthetic rate of *Vigna radiata* plants. Hussain *et al*., (2019) evaluated that SO_4^{2-} application (2 mM) improved stomatal conductance, water use efficiency and activity of Rubisco enzymes in *Vigna radiate* plants under saline environment. The application of 1.5 and 3 g L^{-1} S improved stomatal conductance and photosynthetic efficiency of *Lactuca sativa* under saline environment de Souza Freitas *et al*., (2019). Aziz *et al*., (2019) evaluated that 80 mg kg^{-1} S increased net photosynthetic rate in *Helianthus annuus* prone to saline conditions. Mukhtar *et al*., (2016) reported that application of 5 or 10 g L^{-1} S increased net photosynthetic rate of *Capsicum* spp. under salt stress conditions. Similar to it, an appropriate amount of S showed a positive impact on photosynthesis and plant growth and improved salt tolerance potential of barley plants (Astolfi & Zuchi, 2013).

Previous studies have evaluated different features of salt tolerance mechanisms modulated by exogenously applied S. It has been documented that application of S reduces the Na^+ contents in the plant body, which in turn lowers the harmful effects of salt stress. Nazar (2011) found that S improved growth and development of plants under saline conditions by improving plant nutrients and modulating oxidative enzymes. de Souza Freitas *et al*., (2019) found that application of S (1.5 gL^{-1}) improved photosynthesis, antioxidant activity and Na^+ and K^+ contents and reduced membrane deterioration and Na^+/K^+ ratio in lettuce plants under salt stress conditions.

Sulfur metabolites scavenge the excessive production of reactive oxygen species in saline environment (Fatma *et al*., 2016). Riffat & Ahmad (2020a) reported that the application of potassium sulfate (40 mM) improved the antioxidant activity and balanced the oxidative stress determinants of maize plants under salinity. Saad-Allah & Ragab (2020) found that seed priming with 100 μM S nanoparticles increases chlorophyll contents, nitrogen metabolism, antioxidative activity and ionic contents in salt stressed wheat plants. Sulfur improves cellular activity, plant metabolism and electron transport pathways. It also takes part in antioxidative activity, improves photosynthetic activity and nitrogen metabolism (Capaldi *et al*., 2015).

Application of S fertilizers improves germination, vegetative and yield attributes of plants in salt stress conditions. Sulfur improves the germination of plants reduced by salt stress conditions (Riffat & Ahmad, 2016). Al-Solimani *et al*., (2010) showed that S fertilizers improved protein and oil contents, number of seeds, and yield-related parameters of canola in saline condition. Hence, an adequate supply of S maintains photosynthesis in plants by reducing oxidative damage due to salinity. Moreover, the responses of various plants to S assimilation under saline conditions are shown in Table 1.

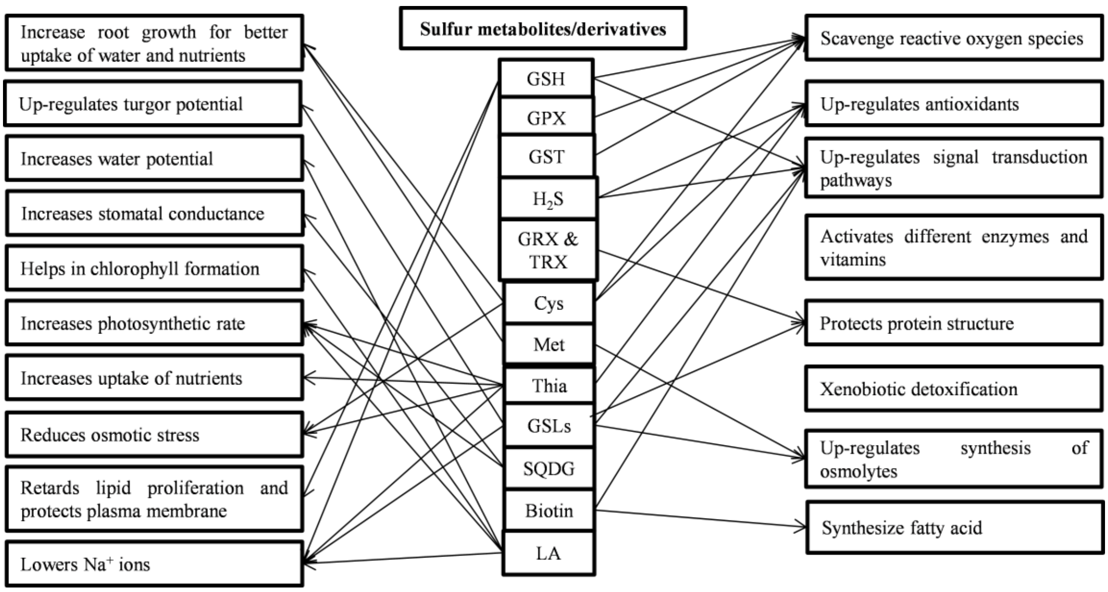
Previous studies reported that the high activity/ quantity of S compounds in saline conditions had a promising contribution in inducing salt tolerance in plants. Different conventional and genetic engineering methods are being employed to increase the activity of different S-containing compounds, *i.e*., ATP-sulfurylase, cysteine, organosulfur, and glutathione to enhance the capability of plants to endure saline environments (Aono *et al*., 1993; Gallardo *et al*., 2014; Perveen *et al*., 2018).

Roles of sulfur metabolites in salt tolerance of plants

Many compounds prepared from S metabolism are beneficial in lowering the harmful effects of abiotic stress due to their power to scavenge free radicals. The compounds comprising of S, modulate physiological processes by up-regulating specific genes to induce tolerance against stresses (Khan *et al*., 2014). Under salinity stress, S metabolites act as antioxidants that neutralize the imbalance in plant cells generated by elevated production of reactive oxygen species. Moreover, S assimilation accelerates the production of S metabolites through the high performance of enzymes involved in the ascorbate-glutathione pathway that develops salinity tolerance in plants (Fatma *et al*., 2016). The role of various S metabolites in alleviating the salt toxicity has been illustrated in (Fig. 2). Following are discussed various metabolites of S having potential to ameliorate the adverse effects of salinity.

Table 1. Response of plants to S assimilation under saline conditions.

Plant	Salt stress (NaCl)	Plant response to S assimilation	Reference
Brassica juncea	50, 100 mmol L^{-1}	High ATP-S activity	Khan *et al.*, 2009
Arabidopsis thaliana	170 mmol L^{-1}	Cysteine contents increased	Romero *et al.,* 2001
Hordeum vulgare	100 mmol L^{-1}	Glutathione activity increased; limited the effect of reactive oxygen species on photosynthesis	Astolfi & Zuchi, 2013
Triticum aestivum	100 mmol L^{-1}	Glutathione contents increased	Khan *et al.*, 2012
Vigna radiata	50 mmol L^{-1}	Increased salinity tolerance	Nazar *et al.,* 2011
Populus × canescens	75 mmol L^{-1}	High glutathione activity protected the photosystem II	Herschbach *et al.*, 2010
Pyrus betulaefolia	150 and 200 mmol L^{-1}	Glutathione stimulation increased	Wu *et al.*, 2009
Phyllanthus amarus	80 mmol L^{-1}	High glutathione concentration	Jaleel *et al.,* 2007
Typha latifolia, Phragmites australis	100 mmol L^{-1}	Cysteine activity increased	Fediuca *et al.,* 2005
Gossypium arboreum	50, 100, and 200 mmol L^{-1}	High glutathione reductase activity	Meloni *et al.*, 2003
Solanum esculantum (=Lycopersicon esculentum)	100 mmol L^{-1}	High glutathione activity	Mittova *et al.,* 2003
Lycopersicon pennellii	100 mmol L^{-1}	Elevation of glutathione contents	Shalata *et al.*, 2001



Abbreviations: GSH = Glutathione; GPX= Glutaredoxins; GST = Glutathione S-transferase; GRX = Glutaredoxins; TRX = Thioredoxins; Cys = Cystein; Met= Methinine; Thia = Thiamine; GSLs = Glucosinolates; SQDG = Sulfoquinovosyl diacylglycerol; LA = Lipoic acid

Fig. 2. Role of S in salt tolerance of plants.

Cysteine: Cysteine is an essential amino acid having a number of key roles in the synthesis of different necessary biomolecules and protection-related proteins in the plant cell. It is the first S-containing organic compound synthesized by plants having a thiol group (Takahashi *et al*., 2011). The thiol side chain is easily oxidized, which is important for its antioxidant property. The oxidation of thiol group forms disulfide bonds with other cysteine side chains which are very important for the structural stability of proteins (Haag *et al*., 2012). Cysteine serves an important function in the formation of protein structure. In a normal cell, its amount is not more than 10-30 µM. Its concentration is enhanced under environmental stresses. It acts as an antioxidant by inactivating free radicals and protects the cell from oxidative harms due to saline conditions (Zagorchev *et al*., 2013). It prepares various compounds that mitigate the adverse effects of salinity plays an important role in forming proteins and enzymes. It serves as a S donor to various vitamins, methionine, co-factors, glutathione and S compounds having significance in the growth and development of plants (Droux, 2004). Cysteine synthesis increases in saline conditions that increase the glutathione synthesis resulting in developing salinity tolerance in plants (Romero *et al*., 2001). In salt-stressed environments, high cysteine synthesis has been reported in *Brassica napus* and *Arabidopsis* that prevents oxidative damage, reduces Na^+ accumulation, improves root elongation, coleoptile length and amylase activity; maintains antioxidant defense system and increases glutathione synthesis to induce salt tolerance (Alvarez *et al*., 2012). Sadak *et al*., (2020) reported that application of cysteine to soya bean plant improved salt tolerance by improving photosynthetic pigments, proline concentration, nitrogen, phosphorous and potassium contents, activities of superoxide dismutase and reduction in H_2O_2 and MDA contents. Nguyen *et al*., (2021) proposed that cysteine not only regulated growth and development of plants but also induced tolerance to salt stress. Various roles of cysteine in improving salt tolerance in plants are shown in Table 2.

Glutathione: Glutathione is a non-protein thiol-containing non-enzymatic antioxidant. It comprises 1-2% of total S in plant body. Its concentration is 0.1-3 mM in plant body. It has very promising roles in plant growth and development in saline conditions. It transports the amino acids through the membrane and plays an important role in sensing reactive oxygen species and signaling pathways that reduce salt toxicity in plants (Aliniaeifard *et al*., 2016). It increases the rate of photosynthesis, improves organic osmolytes, plant dry mass, and yield, and maintains cellular homeostasis in saline conditions (Kattab *et al*., 2007; Hossain *et al*., 2011). Glutathione serves many important functions in plant metabolism, which improves the ability of plants to endure harsh conditions of salt stress. Its antioxidant property retards lipid proliferation and stabilizes the plasma membrane that lowers Na^+ ions to develop salt tolerance. Moreover, it functions as a signaling agent in plants exposed to salt stress (Foyer & Noctor, 2005). Glutathione also scavenges MDA and H_2O_2 produced under salinity stress, thus lowers the concentration of oxidative stress determinants (Wang *et al*., 2014). Hussain *et al*., (2008) proposed that glutathione regulated the seedling growth under saline conditions. Various studies have reported an increase in glutathione activity upon exposure to salt stress. Ruiz & Blumwald (2002) found that wild canola had high tolerance to salt stress by expressing threefold rise in glutathione and cysteine contents in comparison to transgenic plants. Moreover, glutathione detoxify methylglyoxal which indicates its salt tolerance potential (Singla-Pareek *et al*., 2003). El-Shabrawi *et al*., (2010) found that glutathione contents become high under saline conditions in rice genotypes which improve salt tolerance by regulating various antioxidants and nutrient homeostasis. Table 2 is showing various functions of glutathione to reduce salt toxicity.

Thiamine: Thiamine has been shown to have significant roles in saline conditions. There are reports that salinity causes up-regulation of thiamine biosynthesis genes raising thiamine level to endure toxic effects of salinity. Reduction in thiamine-dependent enzymes in plants (grown in saline conditions) cause oxidative stress, and hence supplemental thiamine reduces oxidative stress caused by salinity. Thiamine also has many antioxidative properties. It scavenges free radicals produced during salt stress. Foliar application of thiamine reduces the toxic effects of salinity in plants (Hamada & Al-Hakimi, 2009; Piechocka *et al*., 2019). During salt stress conditions, thiamine improves photosynthetic rate and ultimately plant growth and yield (Cengiz *et al*., 2014), increase cysteine, methionine, and total protein contents that induces salt tolerance, plays a promising role in ionic homeostasis, improves the levels of K^+ Ca^{2+}, P, and N and reduces Na^+ contents, decreases membrane permeability, MDA, H_2O_2 and regulates SOD, POD, and CAT activity (El-Shintinawy & El-Shourbagy, 2001). Moreover, various roles of thiamine under saline conditions are shown in Table 2.

Table 2. Role of S metabolites in salt tolerance of plants.

Sulfur metabolite		Plant	Salinity level	Improvements	References
Cysteine	20 µM	*Hordeum vulgare* cv. Reyan	125 mM	Prevented oxidative damage, had antioxidant properties, limited reactive oxygen species production, maintained cellular homeostasis	Genisel *et al*., 2014
	0.01 µM	*Triticum aestivum* L.	300 mM	Improved antioxidant enzyme activity and K^+/Na^+ ratio, limited Na^+ uptake	Nasibi *et al.,* 2016
	40 mg/L	*Glycine max* L.	3000-6000 mg/L	Enhanced photosynthetic pigments, proline, nitrogen, phosphorous, potassium, superoxide dismutase and catalase contents, reduced hydrogen peroxide and malondialdehyde.	Sadak *et al*., 2020
Glutathione	1 mM	*Vigna radiate* cv. Binamoog-1	200 mM NaCl	Decreased oxidative stress determinants, reactive oxygen species and proline contents, Improved antioxidant activity	Nahar *et al.,* 2015
	0.065mM	*Oryza sativa* L.	200 mM	Improved antioxidants activity and decreased MDA and H_2O_2	Wang *et al.,* 2014
	350 µM	*Lens culinaris* L.	250 mM NaCl	Limited growth inhibition, improved photosynthesis	Gaafar & Seyam, 2018
Thiamine	100 mg/L	*Vicia faba* L.	4.51 dS m^{-1}	Improved plant growth and yield	El-Metwally *et al.*, 2019
	150 µM	*Helianthus annuus* L., *Zea mays* L.	200 mM	Ionic homeostasis, Improved K^+ levels and reduced Na^+ contents, have antioxidant properties, scavenge reactive oxygen species	Hamada & Al-Hakimi, 2009
	100 mg/L	*Zea mays* L.	100 mM	Reduced Na^+, improved K^+, Ca^{2+}, P, and N. Decreased membrane permeability, MDA, H_2O_2 and regulated SOD, POD, and CAT. Improved photosynthetic rate	Kaya *et al*., 2015

Glucosinolates: Glucosinolates are S-containing compounds found in abundance in *Brassica*. It comprises 1-2% of total S in *Brassica* plants. Studies have reported that salt stress improved the activity of glucosinolates in plants, though some findings revealed a reduction in the activity of glucosinolates by increasing salt stress. López-Berenguer *et al*., (2008) reported that by applying 10, and 80 mM NaCl, the activity of glucosinolates was increased in *Brassica oleracea* L. var. *italic*. Similar results have been proposed by Steinbrenner *et al*., (2012), while working on *Brassica rapa* L. However, Golge & Atilla (2017) found that by applying 40, 80, and 100 mM NaCl, the activity of glucosinolates was decreased in *Brassica oleracea* var. italic. In a study, Hassini *et al*., (2016) reported that seed priming with 150 mmol L^{-1} NaCl had no significant effect on the activity of glucosinolates in *Brassica oleracea* var. *capitata*. Previous studies have found that glucosinolates enhance salt tolerance because it causes alteration in plant metabolism in a way to maintain turgor potential through synthesis of various osmoprotectants. Glucosinolates helps plant in osmotic adjustments under low water potential developed under saline conditions (López-Berenguer *et al*., 2007). Glucosinolates serves as signaling agent for activation of the changes in the surrounding cell in salt stressed plants (Pang *et al*., 2012). However, wide research is required to understand the mechanism of glucosinolate regulation in plants.

Methionine: Methionine has significant contribution in ameliorating the toxic effects of a number of environmental stresses through synthesis of different types of polyamines i.e. putrescine, spermidine and spermine. Likewise, the concentration of polyamines has been reported to increase under various environmental stresses such as salinity, drought, cold, UV- radiations, metal toxicity, oxidative stress, and wounding (Farhangi-Abriz & Ghassemi-Golezani, 2016). It improves protein contents in plants and maintains osmotic adjustment to endure saline conditions. Methionine is not only an important constituent of proteins but has a significant contribution in the synthesis of S-adenosyl-methionine that is a major precursor of polyamines and ethylene biosynthesis. It also controls many responses of the plant body *i.e.,* regulation of growth and development of plants, changes in plant morphology, and plays a vital role in plant metabolism that improves plant's ability to cope salt stress (Sadak *et al*., 2015). Methionine is a part of S-adenosyl methionine (SAM) pathway. Under salt stress, SAM synthesis becomes high suggesting that methionine application substantially increases plant salt tolerance (Khan *et al*., 2013; Farhangi-Abriz & Ghassemi-Golezani, 2016).

Sulfoquinovosyl diacylglycerol (SQDG): Sulfoquinovosyl diacylglycerol is a very important S-containing lipid in plants. It constitutes about 3-6% of whole S in leaves (Harwood & Okanenko, 2003) where it is associated with photosynthetic membranes of plants. It has promising role to alleviate the salt stress in plants because it maintains the physiochemical health of plant body that triggers a plant's ability to endure harsh condition of salt stress. Under salt stress conditions, it helps in the proper functioning of chloroplast by maintaining chlorophyll orientation in the membrane, stability of photosystem II and catalytic activity of other photosynthetic enzymes (Okanenko *et al*., 2008). Previous studies have shown that it also helps in the maintenance of growth and activities of PSII in *Synechocystis* sp. PCC 6803 and *C. reinhardtii.* Other reports suggest its central role in maintaining anionic lipids balance in thylakoid membrane (Endo *et al*., 2016) and regulation of glycerolipid biosynthesis, and energy transforming processes in plant cell (Okanenko *et al*., 2008). Substantially higher quantities of SQDG have been found to accumulate in various halophytes to stabilize membrane proteins. Other reports suggest a multifold increase in SQDG (by 15.6% and 22.5%) in *Arabidopsis thaliana* treated with 100 and 200 mM NaCl (Sui & Han, 2014). These results propose that SQDG has a major contribution in cell signaling processes under salinity stress; because it is nearly linked to the photosynthetic apparatus of the plants and thus helps in salt tolerance by coordinating with various plant metabolic processes (Guo *et al*., 2019).

Biotin: Biotin is also known as vitamin B8 or H. Biotin has promising potential in ameliorating the toxic effects of salinity because it maintains structural integrity and have antioxidant property. Under salinity stress, alteration in membrane lipids takes place that affects membrane proteins particularly those involved in cell signaling. Biotin has a central role in regulating synthesis of fatty acid under saline conditions. Hamdia & El-Samad (2000) reported that biotin regulates growth and development in lupine plants prone to salinity stress. The activities of biotin carboxylase, long-chain acyl-CoA synthetase and ketoacyl-ACP synthase increased in *Thellungiella halophile* under saline conditions (Gong *et al*., 2005). Rahman *et al*., (2015) reported a down regulation of biotin carboxylase in salt sensitive genotype of alfalfa; while up regulation was observed in cucumber tissue exposed to salinity (Bajji *et al*., 1998).

Lipoic acid: Lipoic acid contains two S atoms joined by disulphide bond. It is soluble in water as well as in lipids. Due to its dual nature of solubility, it has certain physiological roles both in cell membrane as well as in cytoplasm, thus providing dual-protection to the cellular system (Celik & Ozkaya, 2002). Lipoic acid is a very potent antioxidant. It scavenges reactive oxygen species and free radicles, reduces oxidative stress, acts as a chelating agent to prevent metal toxicity and regenerates glutathione to cope with harsh conditions imposed by salt stress (Jundong *et al*., 2005). It has been reported that external application of alpha lipoic acid improved the activity of photosystem II, improved gene expression of carbon fixation and enzymes involved in chlorophyll metabolism in maize plants in drought stress conditions (Sezgin *et al*., 2019). Lipoic acid is a universal antioxidant that can induce tolerance against salt stress (Yildiz *et al*., 2015). Terzi *et al*., (2018) found that the application of 0.2 mM alpha lipoic acid to maize plants increased leaf water potential and activity of different enzymatic and non-enzymatic antioxidants under osmotic stress. Gorcek & Erdal (2015) reported that lipoic acid prevented the accumulation of Na^+ ions and improved K^+/Na^+ and Ca^{2+} contents in wheat plants exposed to salinity. The conclusive roles ascribed to lipoic acid under saline conditions include a key role in osmoregulation, ionic homeostasis, antioxidant activity and maintains redox state of plant cell. Though plants have been reported to synthesize lipoic acid from octanoic acid, its exact biosynthetic pathway is still unknown (Xiaoa *et al*., 2018).

Role of sulfur salts in improving salt tolerance of plants

Zinc sulfate ($ZnSO_4$): Zinc is an obligatory plant nutrient that helps protect various cellular components. It prevents oxidation of chlorophyll, enhances enzyme function and improves crop yield (Cherif *et al*., 2010). It also has a key role in protein stabilization. According to an estimate, 10% proteins of the biological system need zinc for stabilizing their structure and function. These properties of zinc make it an active nutrient to cope the after effects of salinity. Chemically, $ZnSO_4.2H_2O$ comprises about 35% zinc and is the most commonly used salt of zinc (Tisdale *et al*., 1993). Various application procedures have been practiced to determine $ZnSO_4$ effects under salt stress. It includes soil amendment with $ZnSO_4$ before transplanting and foliar spray. However, foliar application of $ZnSO_4$ is more effective to avoid toxic accumulation of zinc in the soil for relieving salt stress (Jiang *et al*., 2014). Previous findings have reported that application of $ZnSO_4$ alleviates the salinity problem. Zinc sulfate lowers the toxic effects of salinity by detoxifying reactive oxygen species produced under salt stress and improves crop growth and development. It also helps in nutrient translocation and avoids toxic accumulation of Na^+ and Cl^- ions in the plants (Broadley *et al*., 2007; Qu *et al*., 2009). A list of various parameters improved by $ZnSO_4$ in salt stress conditions is presented in Table 3.

Calcium sulfate ($CaSO_4$): Calcium sulfate contains 23% calcium and 19% S and is a by-product of manufacturing superphosphate (Tisdale *et al*., 1993). Calcium is a necessary element that has a variety of roles in abiotic stress tolerance in plants. It is required for many important functions in plants i.e., maintaining structural integrity of plasma membrane, stabilization of cell wall, regulation of cell transport, ion exchange and activates many enzymes (Liu *et al*., 2014). Calcium has been shown to reduce the toxic effects of salinity in plants by having well-defined roles in regulation of metabolism. In saline solution, it is an important source for reducing specific ion toxicity, especially in salt-sensitive crops. It also alters the membrane permeability by increasing electrolytic leakage under salt stress (Bolat *et al*., 2006). Previous findings have reported that calcium plays an important role in improving antioxidant activity, osmotic adjustment and reducing lipid peroxidation in plant cell in saline conditions (Hernandez *et al*., 2003; Amor *et al*., 2010). Various functions improved by $CaSO_4$ under salt stress conditions are shown in Table 3.

Potassium sulfate (K_2SO_4): Potassium sulfate also known as sulfate of potash contains around 50-53% K_2O and 17% S and is water soluble compound (Tisdale *et al*., 1993). Potassium serves an important function in alleviating the toxic effects of Na^+ induced in saline and saline sodic soil by maintaining osmotic regulation and improving the rate of photosynthesis (Daneshian *et al*., 2009). It has been found that application of various potassium fertilizers has improved grain yield under stress condition. Therefore, deleterious effects of salinity can be ameliorated by applying optimized quantities of K_2SO_4. Supplementation with K_2SO_4 helps plants to alleviate toxicity caused by Na^+ ion accumulation, stabilize the membrane proteins and improve nutrient uptake especially that of calcium, potassium and nitrogen (Riffat & Ahmad, 2020c). The improvements in growth attributes of various plants achieved by K_2SO_4 supplementation under salt stress conditions are shown in Table 3.

Ammonium sulfate ($(NH_4)_2SO_4$): Ammonium sulfate contains 24% S and 21% nitrogen. Ammonium sulfate has been recognized as a multi-nutrient fertilizer because of its ability to supply S and nitrogen to crop plants (Williamson *et al*., 2006). Ammonium sulfate is one of the most important acidifying fertilizers because both ammonium and sulfate cause acidity in soil system. Thus, it helps in maintaining pH of alkaline and calcareous soils at appropriate level (Tisdale *et al*., 1993). Ammonium sulfate has potential role in ameliorating salt stress by balancing essential nutrients in plants (Hzhbryan & Kazemi, 2014; Rajaie & Motieallah, 2018). It reduces Na^+ and Cl^- uptake in plants under saline conditions. However, at high concentration, application of $(NH_4)_2SO_4$ increases H^+ and Cl^- ions in the soil that leads to a significant reduction in dry matter production, nutrient uptake and transport and plant yield (Machado *et al*., 2014). The improvement in various growth parameters by application of $(NH_4)_2SO_4$ has been shown in Table 3.

Magnesium sulfate ($MgSO_4$): Magnesium sulfate has 9.8% magnesium and 13% S and is a widely used fertilizer in agriculture system (Tisdale *et al*., 1993). Magnesium has been shown to be effective in reducing the toxic effects of salinity. It regulates the pH and cation-anion balance inside the cell. It serves an important role being the central atom of chlorophyll (Walker & Weinstein, 1991). It is very necessary for ATP synthesis and for aggregation of ribosomes during translation. The length and width of stomata and rate of transpiration increase under optimal magnesium supply that regulates nutrient uptake and translocation in plants. It also helps in synthesis of sugar and transporting starch in the plants that increases plant dry matter. It is readily soluble fertilizer so can be applied both as soil amendment and foliar spray. Exogenous application of magnesium plays an important role in revealing the harmful effects of salinity (Putra *et al*., 2012). However, excessive application of $MgSO_4$ reduces the dry matter production and mineral composition (Kobayashi *et al*., 2005). Various roles of $MgSO_4$ under salt stress are listed in Table 3.

Table 3. Roles of various S salts in improving plant growth and development

Salt	Crop used	Sulfur level applied	Parameters improved	Reference
Zinc sulfate	Spanish lavender	1000, 2000 mgL^{-1}	Essential oils, flavonoids, chlorophyll, stem dry weight	Mehrabani *et al.*, 2017
	Orange	0.2, 0.4%	Leaf mineral content, total chlorophyll, number of fruits per tree, yield, fruit quality	Amro, 2015
	Rice	42-67 mg kg^{-1} soil	Seed germination, root and shoot dry weight	Boonchuay *et al.*, 2013
	Soybean	10-20 µmol L^{-1}	Photosynthetic activity of leaf, dry weight of shoot and root	Jiang *et al.*, 2014
Calcium sulfate	Tomato	2.5, 5 mM	Ca^{2+}, N^{+}, K^{+}, membrane permeability	Tuna *et al.*, 2007
	Plum	2.5, 5 mM	Dry matter, chlorophyll content, K^{+} content	Bolat *et al.*, 2006
	Calligonum mongolicum	5, 10 mM	Plant biomass, photosynthesis, antioxidants, oxidative stress determinants, proline	Xu *et al.*, 2017
Potassium sulfate	Maize	40, 80 mM	Seed germination, plant dry matter, osmolytes and osmoprotectants, K^{+}, Ca^{2+}, NO_3^{-}, PO_4^{2-} contents, yield attributes	Riffat & Ahmad, 2016, 2018a, b, Riffat, 2017, 2018
	Soybean	2.5%	Antioxidant activities, polyphenol, flavonoid, carotenoid, chlorophy	Adhikari *et al.*, 2019
	Tomato	96.8%	Yield, salinity	Carneiro *et al.*, 2017
	Mungbean	75 kg ha^{-1}	Plant height, number of grain pod^{-1} and grain yield	Abbas *et al.*, 2011
Ammonium sulfate	blueberry	0.25 gL^{-1}	Root to shoot dry weight ratio	Machado *et al.*, 2014
	Lemon	100 mg kg^{-1} soil	Dry weight, nutrients	Rajaie & Motieallah, 2018
	Tomato	200 mM	Chlorophyll	Dehnavard *et al.*, 2017
	Tomato	50, 100 mg per kg soil	Dry weight , total acid , vitamin C	Hzhbryan & Kazemi, 2014
Magnesium sulfate	Alfalfa	2-4 g/L	Germination	Abid *et al.*, 2008
	Wheat	60 kg/ha soil	Dry biomass, plant height	El-Zanaty *et al.*, 2012
	Soybean	5% foliar application	Seed yield, protein contents, oil contents	Vrataric *et al.*, 2006
Thiosulfate	Barley	Barley	Dry matter, yield	Morden *et al.*, 1986
	Cassava	Sodium thiosulfate 0.1 mol/L	Flower development, flower longevity, flower number	Hyde *et al.*, 2019
	Arabidopsis, Rice	300 µM	Biomass, gene regulation	Nakajima *et al.*, 2019
	Coleus	Silver thiosulfate 4 mM	Ethylene induced abscission	Baird *et al.*, 1984

Thiosulfates ($S_2O_3^{2-}$): Thiosulfate is an important and readily available form of S that has promising potential in reducing soil pH to lower salt toxicity problem (Stroehlein & Pennington, 1986). Due to its high compatibility with different ions, it remains available to plants over several weeks compared to other forms of S. However, the application of S in elemental form needs oxidation by microbes to become available to plants. When applied in SO_4^{2-} form, it may be lost by leaching as a result of rainfall or water used for irrigation. Thiosulfate supplies S to plants much quicker and for a longer period of time. The thiol group-containing S is very nucleophilic and is appropriate for oxidation-reduction reaction in biological systems. It has been shown to help in ameliorating the oxidative damage caused by salinity (Nazar *et al*., 2011). Sodium thiosulfate is an effective remedy for scavenging the free radical formation in plants grown under salinity stress. It protects the photosynthetic apparatus by preventing chlorophyll degradation (Wang *et al*., 2002). Table 3 shows various roles of thiosulfates for amelioration of salt toxicity problems.

Conclusion

Sulfur has significant importance in plant growth and development because it is a structural constituent of various amino acids, proteins, vitamins, peptides, and sulfo-lipids. Under saline conditions, modulation of S assimilation occurs that activates the detoxification system of plants to scavenge excessive production of reactive oxygen species produced due to salinity. Moreover, the up-regulation of necessary genes protects the plant from harmful damages caused by salinity. Various S metabolites have promising potential in alleviating the toxic effects of salinity by improving ionic uptake, nutrient homeostasis, increasing chlorophyll contents, and activation of the defensive system of plants. Different S salts are used as a source of S and help in alleviating the toxic damages due to salinity. In conclusion, S applied in any form has a promising role in reversing the salt stress by modulating physiological, biochemical, and molecular mechanisms of plants.

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