Chapter 14
Sulfur-Mediated Physiological and Biochemical Alterations to Improve Abiotic Stress Tolerance in Food Crops

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Contents

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Abstract Sulfur (S) is an important macronutrient that plays a significant role in plant growth and development. In the past few decades, efforts focused on reducing sulfur dioxide emission for environment protection had limited the use of S-based fertilizers in agriculture, thereby causing S deficiency in food crops. It also triggered the susceptibility of crop plants to environmental stresses as S assimilation and synthesis of different S compounds modulate several metabolic processes to induce tolerance against various abiotic stresses. The use of inorganic fertilizers containing S has increased tremendously in recent years due to its significance in enhancing crop yield and quality. Therefore, in this chapter, we discuss recent studies on effects of S fertilizers on growth and yield of major cereals (wheat, maize, rice), legumes (mung bean, chickpea, black gram), and oilseeds (sunflower, brassica, soybean). An overview of current state of knowledge on S-mediated physiological and biochemical alterations in food crops may facilitate in developing appropriate fertilizer management strategies to improve yield and quality under abiotic stress conditions.

Keywords Sulfur · Fertilizer management · Environmental stresses · Food crops

Abbreviations

$(NH4)_2SO_4$	Ammonium sulfate
γGCS	Gamma-glutamylcysteine synthetase
ABA	Abscisic acid
ABA	Abscisic acid
AM	Arbuscular mycorrhizal
APX	Ascorbate peroxidase
As	Arsenic
CAN	Calcium ammonium nitrate
$CaSO_4$	Calcium sulfate
CAT	Catalase
Cd	Cadmium
Cr	Chromium
Cys	Cysteine
DHAR	Dehydroascorbate reductase
$FeSO_4$	Iron sulfate
GPX	Glutathione peroxidase
GR	Glutathione reductase
GSH	Reduced glutathione
GST	Glutathione S-transferases
H_2S	Hydrogen sulfide
HMs	Heavy metals
K_2SO_4	Potassium sulfate
Met	Methionine
NaHS	Sodium hydrogen sulfide

Ni	Nickel
PCs	Phytochelatins
ROS	Reactive oxygen species
S	Sulfur
SOD	Superoxide dismutase
Trx	Thioredoxins
Vit	Vitamins
Zn	Zinc
$ZnSO_4$	Zinc sulfate

14.1 Introduction

Sulfur (S) is recognized as the fourth major nutrient after nitrogen (N), phosphorus (P), and potassium (K). It is an essential nutrient required to improve crop yield and quality due to its key role in protein synthesis (Yi et al. 2010). It is the main constituent of proteins, thioredoxin (Trx), methionine (Met), cysteine (Cys), vitamins (Vit), sulfo-lipids (SL), and Fe-S cluster system that play an important role in the regulation of physiological metabolism of plants (Khan et al. 2013). Increased S demand during metabolic adaptation processes suggests the key role of S-containing compounds (Anjum et al. 2015). Metabolism of S influences the accumulation of osmolytes and osmo-protectants (Gill et al. 2013), whereas S-containing compounds such as glutathione (GSH) interplay with signaling pathways to ensure sufficient production of metabolites for ABA synthesis (Herrmann et al. 2014). Sulfate interacts with ABA and acts as a chemical signal to initiate stomatal closure in leaves under water deficit conditions (Hasanuzzaman et al. 2018). Anti-transparent effect of ABA is increased by the presence of sulfate in stomata of plant leaves (Ernst et al. 2010). Assimilation of S results in the formation of several S-containing defense compounds including GSH and phytochelatins (PCs) involved in plant survival under various abiotic stresses (Honsel et al. 2011) (Fig. 14.1). Moreover, interplay of S with phytohormones helps to regulate crucial metabolic processes in plants (Noctor et al. 2012). S metabolism is directly linked to polyamines and ethylene through salvage pathway involved in plant response to drought stress (Sauter et al. 2013). Deficiency of S markedly affects the yield potential of plants even under well-watered conditions (Rasheed et al. 2004). Low S levels in soil influence the uptake of nutrients and nitrate reductase metabolism in plants (Prosser et al. 2001).

Plants uptake S in metabolically inactive form known as sulfate ($SO4^{-2}$) from soil surface. It is reduced into sulfide (S^{-2}) and assimilated into Cys by the activity of ATP sulfurylase (Herrmann et al. 2014). A variety of S compounds such as GSH, Met, and PCs are synthesized from Cys residues which play an important role in alleviating the drastic effects of environmental stresses like drought (Anjum et al. 2015). Sulfur metabolism induces alterations at metabolic and transcriptional levels

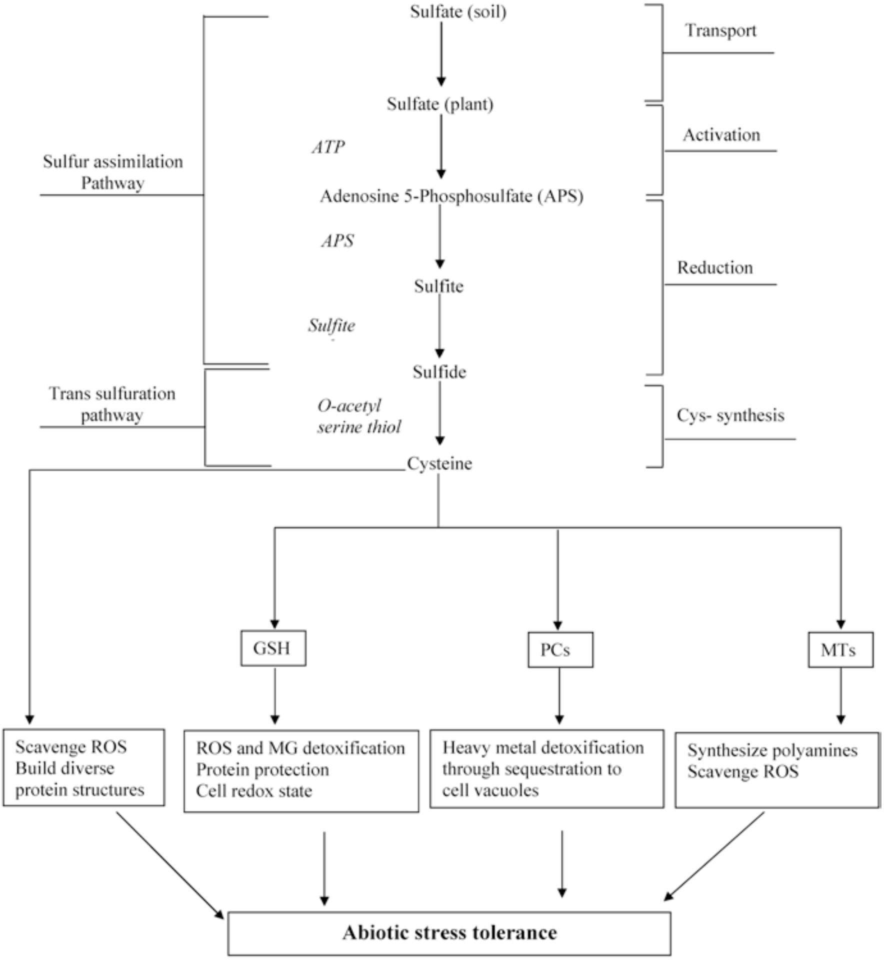

Fig. 14.1 Schematic overview S-mediated physiological and biochemical processes to improve abiotic stress tolerance in crop plants

to activate enzymes and increase root development for maximum uptake of nutrients and water (Ahmad et al. 2016a).

Judicious use of fertilizers and their management is essential to obtain high yield potential in crop plants. Optimum S supplementation significantly influences growth, yield, and quality of plants (Shao et al. 2008). Ahmad et al. (2016b) observed that S supplementation affects N uptake and use efficiency in maize. They applied different levels of S (0, 20, 30, and 40 kg ha^{-1}) in combination with various N application rates (0, 120, and 150 kg ha^{-1}). It was noted that S application significantly increased N uptake in maize at an increasing rate. They recommended S fertilization to improve growth, N use efficiency, and yield of maize. In a greenhouse study, Khan et al. (2015) evaluated the role of S and N fertilization on growth and yield of hybrid sunflower. Although N deficiency delayed all development stages of sunflower, a merked effect of S deficiency was only recorded at floret initiation and anthesis stages. Moreover, S deficiency also reduced Cys and Met by 30% but increased arginine by 34% in achenes. They suggested that timely availability of S is needed to prevent floret abortion in sunflower. Deficiency of S in sunflower at seed filling stage results in kernels with low levels of essential S-containing amino acids. Wani et al. (2001) noted a marked increase in achene yield and quality of sunflower by increasing S doses. A field study on chickpea involving two S sources (gypsum and ammonium sulfate) showed that S supply increased yield by 17% compared to no S application (Islam 2012). It was observed that ammonium sulfate was more efficient than gypsum to improve nutrients uptake and yield in chickpea.

The abovementioned literature highlights the importance of S in plant growth and development. In this chapter, we present a comprehensive overview of S-mediated physiological and biochemical processes involved in improving abiotic stress tolerance in crops (Table 14.1). In addition, comparative effects of different methods of exogenous S supply as well as application of various S sources and their doses are also discussed.

14.2 Role of S in Improving Abiotic Stress Tolerance in Cereals

14.2.1 Wheat

Deficiency of S results in light green to yellow color in young wheat leaves along with stunted growth and spindly stalks. High rainfall and poor drainage during the growth season result in leaching of available S below the root zone. Similarly, fine-textured soils are more likely to be S deficient compared to coarse-textured soil (Shah et al. 2018). Availability of S also facilitates N assimilation in wheat seeds (Tea et al. 2007).

Hydrogen sulfide (H_2S) has emerged as a new stress-signalling molecule with multiple effects on plant metabolism to increase tolerance against various environmental stresses. It is considered an important part of S-induced plant defense mechanisms (Aroca et al. 2018). Application of H_2S donor, i.e., NaHS, was observed to influence ABA metabolism pathway as well as ABA concentration in roots and leaves of wheat seedlings exposed to drought stress (Ma et al. 2016). Moreover, it also upregulated ABA reactivation and catabolism genes in roots. In another study, NaHS application modulated GSH and ascorbate assimilation in wheat leaves under drought stress (Shan et al. 2011). Pretreatment of NaHS markedly decreased malondialdehyde (MDA) content and electrolyte leakage and upregulated dehydroascorbate reductase (DHAR), gamma-glutamylcysteine synthetase (γGCS), glutathione reductase (GR), ascorbate peroxidase (APX), and gamma-glutamylcysteine synthetase (γGCS) compared to no NaHS supply. NaHS-induced upregulation of drought-responsive genes facilitates phytohormones' signal transduction, amino acids'

Table 14.1 Summary of representative reports on the role of S nutrition in improving abiotic stress tolerance in food crops

Sr. #	Crop species	S source and dose	Stage	Stress	Application method	Response	Reference
Legumes							
1	Mungbean	Zinc sulfate (2×10^{-5} M, 3×10^{-5} M, and 4×10^{-5} M)	Before sowing	Salinity stress	Seed priming	Increase in growth and yield	Pandey et al. (2010)
		$ZnSO_4$ (10, 15, and 20 kg ha^{-1})	At sowing	Drought	Soil application	Increase in plant height, yield attributes and protein contents	Usman et al. (2014)
		K_2SO_4 (0, 25, 50, 75, and 100 kg ha^{-1})	Seed bed preparation			Increase in yield	Abbas et al. (2011)
		$FeSO_4$ (5 kg ha^{-1}) and $ZnSO_4$ (10 kg ha^{-1})				Increase in biological yield, grain yield, straw yield, and nodule numbers	Jamal et al. (2018)
		$FeSO_4$	Branching and flowering		Foliar application	Increased growth, yield, and iron and protein contents	Ali et al. (2014)
		Zinc (0 and 0.1%), nitrogen (15 and 25 kg ha^{-1}), and S (0, 20, and 40 kg ha^{-1})	Pre-flowering and pod initiation			Increase in yield and quality of mungbean	Muniswamy et al. (2018)
2	Chickpea	$ZnSO_4$	Before sowing	Salinity stress	Seed priming	Increase in germination and early seedling growth	Seyedi (2011)
		$ZnSO_4$ (0, 20, 50, and 100 mg L^{-1})				Increased dry mass, seed Zn content, and Zn uptake and translocation	Nautiyal and Shukla (2013)
		Gypsum and ammonium sulfate	At sowing	Drought stress	Soil application	17% increase in yield	Islam (2012)
		Zinc sulfate	Pre-flowering	Zn deficiency		Reduces flower abortion, infertility of pollen and ovule	Pathak et al. (2012)
		K_2SO_4 (1.5%) and CAN (2 and 3%)	40 and 60 DAS	Terminal drought	Foliar application	Increase in yield and yield attributes	Mahmood et al. (2017)
3	Black gram	2% DAP, 1% KCL, 1% boron, 1% $MgSO_4$, 1% $ZnSO_4$	30 and 45 DAS		Foliar application	Increase in yield and yield attributes	Maheswari and Karthik (2017)

Cereals							
4	Wheat	Sodium hydrosulfide (NaHS, H_2S donor) (500 μM)	Two leaf seedling stage	Drought stress	(Solution form) Foliar application	Improves physiological characteristics, regulated ABA catabolism, and biomass accumulation	Ma et al. (2016)
		Sodium hydrosulfide (NaHS, H2S donor) 1 mM	Three leaf seedling stages		Pretreatment in solution for 12 h	Regulates the glutathione and ascorbate metabolism	Shan et al. (2011)
		Elemental sulfur (0, 25, 50, and 75 kg ha^{-1})	Before sowing	Salinity stress	Soil application	Increase in K/Ca contents and yield and yield attributes	Ali et al. (2012)
		$CaSO_4$ (0, 50, 100, 150, 200 kg ha^{-1})	Before sowing		Soil application	Positive correlation between K/Ca and increase growth and yield	Arshadullah et al. (2013)
		K_2SO_4 (0. 50, 100, 150, 200 mM) of	Two weeks after sowing (seedling stage)		Fertigation method	Increases nutrient content and biomass accumulation	Kausar et al. (2016)
		Ammonium sulphate $(NH_4)_2SO_4$ (0, 1, 5, and 10 mM)	Two leaf stages	Cadmium (Cd) stress	Fertigation	Increased chlorophyll content, total carbohydrate accumulation, and antioxidant enzyme activity	Gaafar et al. (2012)
		Elemental sulfur + Se (0, 200 mg S kg^{-1})	Before sowing		Soil application	Regulates ethylene formation and proline and GSH metabolism and improves photosynthesis and growth	Khan et al. (2014)
		NaHS (H_2S donor) (0.4, 0.8, 1.2 mM)	Seedling stage	Copper stress	Fertigation	Increased the value of antioxidants, UPSII, Pn, Fv/Fm, qN, and qP in wheat leaves which alleviate Cu stress	Dai et al. (2016)
5	Rice	NaHS (H_2S donor) (0.75 mmol/L)	Before sowing	Drought stress	Seed priming	Improves soluble protein content and lowers osmotic potential, membrane stability, higher germination potential, and germination rate	Liu et al. (2017)

(continued)

Table 14.1 (continued)

Sr. #	Crop species	S source and dose	Stage	Stress	Application method	Response	Reference
		Gypsum (100 soil gypsum requirement)) and elemental sulfur (0, 25, 50, 75, 100, and 125% of SGR)	30 days before sowing and 10 days after transplanting	Salinity stress	Soil application	Maintains oxidative metabolism and mineral homeostasis and improves chemical properties of soil and crop yield	Ahmed et al. (2016)
		NaHS (H_2S donor) (0, 25, 50, 100, and 200 μM)	Twelve-day-old seedling		Pretreated with solution	Regulates minerals homeostases, improves biochemical and physiological processes, and increases growth and production	Mostofa et al. (2015)
		(S° and $SO^{-2}{}_4$) (0, 30, and 120 mg S kg^{-1})	Before sowing	Arsenic stress	Soil application	Improves tolerance against AS stress	Hu et al. (2007)
		$ZnSO_4$ (control, 13 kg ha^{-1})	Panical initiation, milky stages	Cadmium (Cd) stress	Soil and foliar application	Improves yield and yield attributes in rice	Fahad et al. (2015)
		Elemental sulfur (0, 60, and 120 mg kg^{-1})	Before sowing		Soil application	Decreases Cd toxicity in rice	Fan et al. (2010)
		NaHS (H_2S donor) (100 and 200 μM)	Seedling stage	Mercury (Hg) stress	Pretreated with solution for 24 h	Scavenges peroxy radicals and improves seedling growth	Chen et al. (2017)
6	Maize	(0, 250, 500, 750, and 1000 kg ha^{-1})	At sowing	Salinity stress	Soil application	Enhances yield components and grain production	Manesh et al. (2013)
		K_2SO_4 (0, 20, 40, 60, 80, and 100 mM			Soil application	Improved all germination parameters and decreased time for 50% germination time	Riffat and Ahmad (2016a, b)
		H_2S (0.6 mM NaHS)	Seedling stage		Pretreatment	Reduces electrolyte leakage and malondialdehyde content and increases salt stress tolerance	Shan et al. (2014)

		Elemental sulfur	Before sowing	Zinc stress	Hoagland solution form	Improves leaf chlorophyll contents and physiological characteristics in maize	Xu et al. (2008)
		Elemental S (0, 32, 160, 640 mg kg^{-1})	Before sowing		Soil application	Increases antioxidant enzyme activity and improves tolerance against zinc stress	Cui and Zhao (2011)
					Soil application	Increases activity of CAT and POD and MDA content	Cui and Wang (2006)
		Elemental S (control and 50 mmol kg^{-1} S)	Before sowing	Cadmium (Cd) stress	Side dressing in soil	Increases growth and yield of maize	Sajedi et al. (2010)
		$ZnSO_4$ (0, 25, and 45 kg ha^{-1})	Sowing time	Drought stress	Foliar application	Improves drought tolerance and yield of maize	Shahzad et al. (2017)
		K_2SO_4 (control, 1, 2, and 5%)	(15 and 7 days before pollination)		Foliar application	Increases yield and yield components	Vazin (2012)
		(0, 250, 500, 750, and 1000 kg ha^{-1})			Soil application	Enhances yield components and grain production	Manesh et al. (2013)
		K_2SO_4 (0, 20, 40, 60, 80, and 100 mM	At sowing	Salinity stress	Soil application	Improved all germination parameters and decreased time for 50% germination time	Riffat and Ahmad (2016a, b)
		H_2S (0.6 mM NaHS)	Seedling stage	Salinity stress	Pretreatment	Reduces electrolyte leakage and malondialdehyde content and increases salt stress tolerance	Shan et al. (2014)
		Elemental sulfur	Before sowing	Zinc stress	Hoagland solution form	Improves leaf chlorophyll contents and physiological characteristics in maize	Xu et al. (2008)
		Elemental S (0, 32, 160, 640 mg kg^{-1})	Before sowing	Zinc stress	Soil application	Increases antioxidant enzyme activity and improves tolerance against zinc stress	Cui and Zhao (2011)
		Elemental S (control and 50 mmol kg^{-1} S)	Before sowing	Cadmium (Cd) stress	Soil application	Increases activity of CAT and POD and MDA contents	Cui and Wang (2006)

(continued)

Table 14.1 (continued)

Sr. #	Crop species	S source and dose	Stage	Stress	Application method	Response	Reference
Oilseed crops							
7	Sunflower	$ZnSO_4$ (15, 30, 45, 60, and 75 kg ha^{-1})	At sowing	Zn deficient	Soil application	Increased growth and yield	Cheema et al. (2014)
		$FeSO_4$ (0, 2, and 4 ppm)	Vegetative stage	Drought stress	Foliar application	Increased growth and yield	Ebrahimian and Bybordi (2011)
		$ZnSO_4$ (0, 0.5, and 1%)	Vegetative and reproductive			Increased seed yield	Shahri et al. (2012)
		$FeSO_4$ (0 and 100 mM)	Seedling stage	Salinity stress		Increased net CO_2 assimilation rate, leaf area, shoot dry weight, chlorophyll content, and iron content	Torabian et al. (2017)
8	Brassica	S-deficient and S-sufficient soils	Early growth stage	Cd stress	Soil amendment	Increased activities of glutathione reductase, ascorbate peroxidase, and catalase	Bashir et al. (2015)
		$ZnSO_4$ and $MnSO_4$ (3000 and 4000 mg L^{-1})	Seedling stage	Drought stress	Foliar application	Improved growth attributes and biochemical aspects	Khan et al. (2016)
		Ammonium sulfate (0.4, 0.6, and 2%)	Pod initiation		Foliar application	Increased yield and yield attributes	Khalid et al. (2018)
		Sulfur (40 kg ha^{-1}) and thiourea (500 and 1000 mg L^{-1})	Rosette, bud formation, and flowering stage		Foliar (thiourea) soil application (sulfur)	Increased growth yield and quality	Rehman et al. (2013)

9	Soybean	3% $ZnSO_4$, 3% $FeSO_4$, and 3% $ZnSO_4$ + 3% $FeSO_4$	Before sowing	Drought stress	Seed priming	Increased physiological attributes	Dehnavi and Sheshbahre (2017)
		Mo (400 ppm) and $FeSO_4$ (400 ppm)	Reproductive stage	Drought stress	Foliar application	Improved yield and yield attributes	Heidarzade et al. (2016)
		K_2SO_4 (2.5%)	Early growth stages	Salinity stress	Foliar application	Improved plant growth, flavonoids, total phenols, antioxidant activity, carotenoids, and chlorophyll contents	Adhikari et al. (2019)

metabolism, and translocation of iron from root to shoot to improve drought tolerance in wheat (Liu et al. 2017).

Salinity stress severely hampers wheat growth and productivity. Exposure to salt stress of 6–8 dS m^{-1} causes a marked reduction in wheat yield (Royo and Abió 2003). S-containing compounds play a significant role in enhancing salinity tolerance through upregulation of specific genes and modulating several physiological and biochemical processes (Khan et al. 2014). A negative correlation was observed between sodium (Na) content and S application in wheat exposed to saline-sodic soil (Ali et al. 2012). Increasing S doses (0, 25, 50, and 75 kg ha^{-1}) significantly improved nutrient uptake and yield of wheat resulting in high K and calcium (Ca) content in grains to alleviate salinity/sodicity. In a similar study, Arshadullah et al. (2013) observed a negative correlation between Ca and Na ions in wheat plants treated with different doses of $CaSO_4$ (0, 50, 100, 150, 200 kg ha^{-1}) under saline-sodic soil (ECe = 5.32 dS m^{-1}). In contrast, K and Ca ions were positively correlated resulting in maximum wheat yield by application of 150 kg ha^{-1} $CaSO_4$. Recently, Kausar et al. (2016) reported a marked increase in nutrient uptake and biomass accumulation by treating wheat plants with various K_2SO_4 doses (0.50, 100, 150, 200 mM) under saline conditions.

Heavy metal (HM) contamination of agricultural soils is a major concern for plant scientists due to potential harms on animals and human health. Wheat is a major food crop in most parts of the world, and high concentration of HMs in wheat grains poses serious health risks (Ivezić et al. 2013). Toxic concentrations of cadmium (Cd), nickel (Ni), chromium (Cr), lead (Pb), and zinc (Zn) in wheat flour may cause health disorders like kidney and liver failure. Treatment of seedlings with different S concentrations (0, 1, 5, and 10 mM) was observed to reduce MDA content, improved growth attributes, and increased total carbohydrate accumulation in wheat exposed to Cd toxicity (Gaafar et al. 2012). Khan et al. (2015) evaluated combined effects of S and Se to minimize Cd toxicity in wheat. A significant increase in Cd tolerance was correlated with GSH and proline synthesis due to reduced activity of proline oxidase (PROX) and high glutamyl kinase (GK) activity in leaf tissues. Pretreatment with NaHS (0, 0.4, 0.8, and 1.2 mM) was observed to improve PSII photochemistry, photochemical quenching, and antioxidative activities in wheat seedlings exposed to copper (Cu) stress (Dai et al. 2016). Environmental pollutants like nickel (Ni) interfere with uptake and distribution of mineral nutrients including S to reduce growth and quality of wheat. Matraszek et al. (2016) conducted a series of water culture experiments to evaluate the effects of Ni toxicity on macronutrient composition in wheat. They found that intensive S-SO_4^{2-} nutrition partially improved biomass, enhanced ionic equilibrium, and increased nutrient accumulation in shoots of wheat plants exposed to Ni toxicity.

14.2.2 Maize

Deficiency of S has been more prevalent in maize in recent past due to reduced deposition of atmospheric S, use of crop residues, and no tillage. Low S supply results in yellowing of leaves including interveinal chlorosis. Application of poultry manure may somewhat supplement the soil with organic S however; it needs to undergo mineralization by soil microorganisms to make it available for plants. Microbial inoculation in combination with inorganic S fertilizers has also been found effective in maize. Combined effects of zinc sulfate ($ZnSO_4$) and vesicular arbuscular mycorrhizal (AM) fungus on biomass accumulation and production of maize were investigated by Sajedi et al. (2010). The plants were applied with three different levels of $ZnSO_4$ (0, 25, and 45 kg ha^{-1}). The results showed that maize growth is not significantly affected by AM fungus under well-watered conditions. However, increasing level of $ZnSO_4$ in combination with AM fungus significantly improved maize biomass and yield under water deficit conditions. They concluded that combined application of $ZnSO_4$ (45 kg ha^{-1}) and AM fungus might be utilized as an effective approach to improve growth and yield of maize. A recent report by Shahzad et al. (2017) showed that foliar application of K_2SO_4 reduces pre-anthesis abortion of maize kernel resulting in higher yield under drought stress conditions. In another study, Vazin (2012) found that foliar application of various $ZnSO_4$ doses (0, 0.5%, 1%, and 1.5%) markedly improved yield attributes of maize under water deficit conditions.

High accretion of Na^+ in the leaves is one of the main reasons for susceptibility of maize to salinity stress (Farooq et al. 2015). Accumulation of Na^+ markedly reduces K content in symplast of maize leaves that disturbs stomatal undulations under saline conditions (Jafar et al. 2012). Exposure to salt stress induces high Cys production due to increased activity of O-acetylserine (thiol) lyase (OASTL) leading to better salt tolerance in plants (Fediuc et al. 2005). In a pot study, Riffat and Ahmad (2016a) found a significant effect of S application on biomass accumulation and nutrient content of maize seedlings exposed to salt stress. In another study, they observed a marked increase in germination attributes of different maize cultivars treated with K_2SO_4 under saline conditions (Riffat and Ahmad 2016b). High S supply may cause a reduction in maize yield under salinity stress as reported by Manesh et al. (2013). Maize plants were subjected to saline environment (water salinity 9.79 dSm^{-1} and soil salinity 9.3 dSm^{-1}) and treated with various S doses, i.e., 0, 250, 500, 750, and 1000 kg ha^{-1}. Exogenous S supply up to 750 kg ha^{-1} caused a linear increase in maize yield; however, higher S dose of 1000 kg ha^{-1} markedly reduced the yield. Shan et al. (2014) suggested that application of S sources like H_2S helps to maintain the redox states of ascorbate and GSH to prevent electrolyte leakage that ultimately enhances salt tolerance in maize. Increased GSH content in roots of salt-stressed maize seedlings may be ascribed to high salt tolerance (AbdElgawad et al. 2016), which may also serve as a signal for ABA biosynthesis in shoot (Bittner et al. 2001). Maize seedlings exposed to S deficiency exhibited a marked increase in catalase (CAT) and superoxide dismutase (SOD) activities in leaf sheaths and blades due to increased ROS production under salinity stress (Chorianopoulou et al. 2012).

High concentration of toxic metals in agricultural soils has severely affected yield and nutritive value of maize. Availability of S plays a pivotal role in enhancing tolerance to metal toxicity through regulation of electron transport chain in Fe-S clusters and detoxification of HMs and xenobiotics (Hell and Hillebrand 2001). Efficacy of applied S doses may vary with the soil depth as both sulfate and elemental S exhibited a stronger effect at 0–40 cm soil layer compared to 40–80 cm horizon (Skwierawska et al. 2012). Applied S doses did not significantly affect Cu and Mn content, whereas they increased Cd and reduced Ni content in soils at a depth of 0–40 cm. Xu et al. (2008) observed toxic effects of high Zn content on pigments of maize seedlings. Supplementation of S in nutrient solution mitigated Zn toxicity and reduced the damage to young seedlings. In a similar study, Cui and Zhao (2011) reported positive effect of S application on antioxidative activities of CAT and SOD to alleviate Zn toxicity in maize seedlings. Contrarily, treatment with 50 mmol kg^{-1} S markedly reduced CAT and peroxidase (POX) activities in leaves of maize seedlings exposed to Cd toxicity suggesting that plant response to metal toxicity varies with intensity of stress, metal concentration, and plant species (Cui and Wang 2006).

14.2.3 Rice

Rice (*Oryza sativa* L.) is a staple food of nearly half of the world's population; hence, it is imperative to overcome challenges limiting rice productivity worldwide. S deficiency rarely occurs in irrigated rice and usually affects vegetative stage. It is essential to evaluate the S requirement of rice crop since low S availability results in reduced protein synthesis and causes delayed plant development and maturity (Tsujimoto et al. 2017). In contrast, high S supply may result in reduced nutrient uptake and root respiration due to sulfide toxicity, particularly in low Fe soils. Rice is considered sensitive to drought stress due to presence of shallow root system, little circular wax, and rapid stomatal closure under water deficit conditions (Ji et al. 2012). Liu et al. (2017) evaluated the effect of NaHS on antioxidative mechanism of rice seedlings subjected to PEG-induced oxidative stress. Pretreatment with NaHS markedly enhanced germination rate and prevented the degradation of soluble protein content. In addition, it significantly reduced accumulation of H_2O_2 in seeds and helped to maintain cell membrane stability resulting in slow disintegration and senescence of seedlings.

Among cereals, rice is considered the most sensitive to salinity stress. Exposure to salt concentration of even less than 40 mM may cause a significant loss in rice growth and productivity (Munns and Tester 2008). Apoplastic uptake and distribution of Na^+ cause toxicity which may be prevented by rapid downregulation of OsHKT2;1 in rice roots. An important GSH transporter in rice (OsGT1) is weakly expressed under normal conditions suggesting that it may play a key role in S transport under environmental stresses like salinity (Zhang et al. 2004; Srivalli and Khanna-Chopra 2008). S starvation reduced GSH level by 70% in rice seedlings that ultimately decreased PSII efficiency and the ability of PSI to photoreduce $NADP^+$ by 31 and 61%, respectively. However, no significant effect of S deficiency was observed on metabolites of Calvin or tricarboxylic acid (TCA) cycle (Lunde et al. 2008). Ahmed et al. (2016) found that S fertilization markedly improved rice yield under saline conditions. A positive effect of S application was also noted on soil chemical properties such as such as SAR, pH, and ECe. Maintenance of Na^+/K^+

balance was observed to increase salt tolerance in rice seedlings treated with NaHS (Mostofa et al. 2015). Supplementation of this H_2S donor also helped to maintain oxidative metabolism and mineral homeostasis by inhibiting Na^+ uptake in the seedlings.

Consumption of rice contaminated with toxic metals may cause serious health hazards in humans. Low S availability affects oxidative thiol modifications, thereby increasing HM translocation from root to shoot (Leichert et al. 2008). In young rice seedlings, S application was reported to increase Fe and Mn accumulation in rhizosphere to reduce arsenic (As) toxicity (Wu et al. 2014). S availability positively influences thiol metabolism and glycolytic enzymes to promote amino acid accumulation in leaves of rice seedlings exposed to AS toxicity (Dixit et al. 2015). Fahad et al. (2015) found that application of $ZnSO_4$ in combination with rubber ash alleviated Cd toxicity in different rice cultivars. Foliar application of $ZnSO_4$ at panical initiation and milking stages significantly increased the number of spikelets and panicles as well as spikelet fertility to improve grain yield by 73% under salt stress conditions. In a similar study, Fan et al. (2010) observed significant reduction in Cd accumulation in brown rice by excessive S supply. Pretreatment of rice seedlings with NaHS was reported to reduce mercury (Hg) toxicity in rice seedlings exposed to $HgCl_2$ (100 μM) for 3 days (Chen et al. 2017). The seedlings treated with NaHS exhibited increased expression of prominent thiol-containing compounds (OsMT-1 and NPT) to prevent Hg transport from root to shoot. Moreover, NaHS supplementation helped to scavenge or inhibit H_2O_2 and O_2^- (peroxy radicals) as well as CAT or SOD inhibitors (AT and DDC) even in the presence of Hg.

14.3 Role of S in Improving Abiotic Stress Tolerance in Legumes

14.3.1 Mung Bean

Pulses are part of healthy and balanced human diet and play an *important* role in preventing many acute diseases. They belong to family Leguminosae so they also increase soil C and N, reduce soil erosion, and help to control soil pathogens (Bagayoko et al. 2000; Sainju et al. 2005). Moreover, legumes positively influence growth of the following crops when grown in rotations with cereals. Hence, promoting legumes cultivation in developing countries can be an effective approach to reduce poverty and hunger in poor or developing countries (Abate et al. 2012).

Mung bean is an important pulse crop or food legume that is grown primarily for dry seeds and very occasionally used as a forage (Tomooka 2002). Although mung bean is considered tolerant to limited water supply, low water availability at reproductive and grain filling stages significantly reduces its yield and quality (Ahmad et al. 2015). Exposure to drought stress after 6 weeks of sowing can lead to decline in number of leaves, root nodules, dry matter, and plant height of mung bean (Ranawake et al. 2011). Reduction in plant production under drought stress is related to reduction in absorption, translocation, and redistribution of nutrients (Rouphael et al. 2012). Drought stress increases the concentration of sulfate compared to other ions like phosphate or nitrate, providing evidence that sulfate demand increases under limited water conditions (Ernst et al. 2010). Sulfate interacts with ABA and acts as a chemical signal to initiate stomatal closure in leaves under water deficit conditions. Usman et al. (2014) evaluated the role of $ZnSO_4$ (10, 15, and 20 kg ha^{-1}) on growth and yield of mung bean and reported a significant increase in growth and yield attributes. It was found that soil application of 20 kg ha^{-1} $ZnSO_4$ resulted in maximum growth and yield attributes. However, soil applied $ZnSO_4$ (15 kg ha^{-1}) resulted in maximum plant height. In addition, protein content was found higher in plants supplemented with 10 kg ha^{-1} $ZnSO_4$.

Recently, Jamal et al. (2018) reported that application of $FeSO_4$ at 5 kg ha^{-1} in combination with $ZnSO_4$ at 10 kg ha^{-1} significantly improved the biological yield, grain yield, straw yield, and nodule numbers in mung bean. Similarly, application of K_2SO_4 significantly improved yield and yield attributes in mung bean grown under arid climate (Abbas et al. 2011). Ali et al. (2014) suggested that foliar spray of iron sulfate ($FeSO_4$) at branching and flowering stages can significantly increase the growth and yield attributes of mung bean. In addition, protein and iron contents of mung bean plants supplemented with S were also found higher compared to control plant, i.e., no S supply. Muniswamy et al. (2018) evaluated the role of foliar applied Zn (0 and 0.1%), N (15 and 25 kg ha^{-1}), and S (0, 20, and 40 kg ha^{-1}) on yield and quality of mung bean. They reported that application of 25 kg ha^{-1} N combined with 40 kg ha^{-1} S and 0.1% Zn (at both pre-flowering and pod initiation stages) markedly increased yield and quality of mung bean.

Salinity stress in mung bean leads to significant reduction in yield (Saha et al. 2010) due to poor germination and seedling growth (Promila and Kumar 2000; Misra and Dwivedi 2004). In a pot study, Pandey et al. (2010) found that exogenous $ZnSO_4$ application may reduce the suppressing effects of salt stress on growth of mung bean seedlings. Similarly, Pandey et al. (2010) compared the effects of $ZnSO_4$ seed treatment and foliar spray on mung bean under induced salt stress conditions. They observed that seed priming and foliar spray of $ZnSO_4$ are effective strategies to alleviate the harmful effects of salt stress in mung bean.

Toxic metals negatively affect microbial population in the soil and may affect population size, diversity, and overall activity of soil microbiota (Kelly et al. 2003). Among various HMs, silver (Ag) and Pb were found to exert the most toxic effects on growth of soil microorganisms that delayed seed germination in mung bean (Ashraf and Ali 2015). They found that application of $ZnSO_4$ positively influenced microbial population and helped to increase germination percentage under Ag or Pb toxicity. Positive effects of S supply on microbial population in a mung bean field were also reported by Bahadur and Tiwari (2014). They observed that application of 15 kg ha^{-1} S increased *Rhizobium* and *Azotobacter* population that ultimately increased grain yield in mung bean. Recent reports of Islam et al. (2017) indicate that S supply in combination with boron (B) was more effective than individual application of these nutrients to improve grain yield in mung bean.

14.3.2 Chickpea

Seed proteins in chickpea, like other legumes, are deficient in S-containing compounds such as Cys, Met, and amino acids (Chiaiese et al. 2004). Exogenous S supply significantly improves accumulation of S-enriched seed proteins in legumes including chickpea (Sexton et al. 1998). In a controlled study, Chiaiese et al. (2004) found that addition of a transgene, sunflower seed albumin (SSA), encoding Cys and Met reduced accumulation of S-containing amino acids in chickpea seeds. Excess S supply downregulated SSA expression and improved seed protein composition in chickpea. S deficiency also leads to flower abortion and infertility of pollen and ovule resulting in low yield in chickpea. Combined application of K_2SO_4 and calcium ammonium nitrate (CAN) was observed to ameliorate negative effects of drought stress on yield attributes of chickpea (Mahmood et al. 2017). Application of 1.5% K_2SO_4 + 2 and 3% CAN resulted in maximum increase in yield and yield attributes when applied at 40 and 60 days after sowing.

Chickpea is considered sensitive to salinity as exposure to salt stress results in poor germination and seedling growth (Zawude and Shanko 2017). Seyedi (2011) conducted a laboratory experiment to evaluate the role of S supply in improving salinity tolerance in chickpea. They observed that chickpea seeds primed with $ZnSO_4$ exhibited enhanced germination and seedling establishment under saline conditions. In a similar study, Nautiyal and Shukla (2013) found that S supplementation improved seedling dry mass, seed Zn content, as well as Zn uptake and translocation in salt-stressed chickpea plants raised from $ZnSO_4$-primed seeds. Positive effects of S application were found related with increased carbonic anhydrase and SOD activity in $ZnSO_4$-treated seeds. Islam (2012) conducted a field trial to evaluate the comparative effects of two different S sources, viz., gypsum and $(NH_4)_2SO_4$, on yield of chickpea. They found that exogenous S supply improved yield by 17%; however, $(NH_4)_2SO_4$ was found more effective than gypsum regarding increment in nutrient uptake and yield.

14.3.3 Black Gram

Pulse crops, viz., black gram, green gram, cowpea, and horse gram, exhibited increased yield when supplemented with foliar spray of nutrient solution containing 2% DAP, 1% KCl, 1% boron, 1% $MgSO_4$, and 1% $ZnSO_4$ at 30 and 45 DAS of pulse crop (Maheswari and Karthik 2017). Patel et al. (2018) evaluated the effects of different S sources, viz., elemental S, gypsum, and ammonium sulfate, and S levels, viz., 0, 20, 40, and 60 kg S ha^{-1}, on growth and yield of black gram. Among different sources, gypsum was found superior in terms of growth and yield. Among various levels, 40 kg ha^{-1} gypsum was found more superior compared to others. Srivastava and Shukla (2016) reported an adverse effect of arsenic (As), cadmium (Cd), cobalt (Co), chromium (Cr), and lead (Pb) on growth of black gram. They found that heavy metal toxicity followed the order As > Cr > Cd > Co > Pb in terms of damage caused to black gram plants. Plants grown in As toxic soils failed to survive and wilted within 1 week. A significant loss of pigments and proteins was noted in plants exposed to Cr and Co toxicity compared to control plants. Antioxidant enzymes' activity was found higher in plants grown in Cr and Co toxic soils compared to Cd and Pb plants. It was concluded that black gram is highly sensitive to As followed by Cr and Pb was found least toxic for growth.

14.4 Role of S in Improving Abiotic Stress Tolerance in Oilseeds

14.4.1 Sunflower

Sunflower seeds are used to make high-quality vegetable oil (Okoko et al. 2008). Its yield depends upon the availability of water at different growth stages, and flowering stage is considered as most critical stage regarding water availability. It was reported that application of S at the rate of 25 kg ha^{-1} significantly improved the plant height, head diameter, no. of seeds per achene, biological yield, and achene yield of sunflower plants (Poonia 2000). Wani et al. (2001) suggested that increasing S doses might significantly improve seed yield and quality of sunflower seeds. Recently, Ullah et al. (2019) found a significant increase in sunflower yield by applying S in combination with K. The maximum grain yield and oil quality were recorded in plants supplemented with 60 kg ha^{-1} S + 90 kg ha^{-1} K. Similarly, S fertilization combined with exogenous Zn supply alleviated the adverse effects of drought stress at different growth stages of sunflower (Zafar et al. 2014). Application of S using gypsum at the rate of 60 kg ha^{-1} not only increased the plant height, leaf area index, and dry matter of sunflower but also improved the pH of the soil (Usha Rani et al. 2009). Cheema et al. (2014) investigated the effects of various $ZnSO_4$ concentrations (15, 30, 45, 60, and 75 kg ha^{-1}) on sunflower. They reported that plants supplemented with 45 kg ha^{-1} $ZnSO_4$ resulted in maximum stem diameter, number of achenes per head, achene yield, head diameter, and biological yield. Moreover, harvest index and 1000-achene weight were found maximum in plants supplemented with 60 kg ha^{-1} $ZnSO_4$. A study involving exposure of sunflower to drought stress at vegetative and reproductive stages showed that foliar application of 1% $ZnSO_4$ significantly ameliorated water stress to improve achene yield in sunflower (Shahri et al. 2012). Likewise, foliar application of $FeSO_4$ was found helpful in improving growth and yield of sunflower under normal and drought stress conditions (Ebrahimian and Bybordi 2011).

Nano-particles of $FeSO_4$ were found to significantly reduce salt-induced oxidative stress in sunflower (Torabian et al. 2017). S supplementation markedly reduced Na^+ content and increased net CO_2 assimilation rate, leaf area, shoot dry weight, chlorophyll content, sub-stomatal CO_2 concentration, and Fe content to improve salinity tolerance in sunflower.

14.4.2 Brassica

In general, *Brassica* species require S at vegetative stage to synthesize essential proteins for improved oil quality (Blake-Kalff et al. 2001). It is estimated that production of 1 ton rape seed requires about 16 kg S compared to wheat seed that only requires 2–3 kg S (Lee et al. 2016). Moreover, these species contain high amount (20%) of organic S in the form of S-containing metabolites like glucosinolate (Aghajanzadeh et al. 2014). Deficiency of S significantly reduces the incorporation of total amount of S into proteins by 62% (Lee et al. 2013). A study involving two contrasting *Brassica napus* species, viz., Mosa and Saturnin, showed that genotype possessing better sulfur use efficiency exhibited higher tolerance to drought stress (Lee et al. 2014). Dhruw et al. (2017) found that application of S using $ZnSO_4$ (40 kg ha^{-1}) along with basal dose of N-P-K @ 120:60:40 can significantly improve growth, yield, and oil contents of *B. juncea* plants. A field study by Mishra et al. (2010) showed that S fertilization in combination with P resulted in maximum mustard oil production. Khan et al. (2016) compared the effects of $ZnSO_4$ and manganese sulfate ($MnSO_4$) in improving drought tolerance in *B. juncea.* They reported a significant increase in growth attributes, biochemical aspects (chlorophyll and carotenoids), and relative water content of *B. juncea* treated with S under drought stress.

Salt stress tolerance in *Brassica* species is related to modulation in several physiological and biochemical processes (Ashraf and McNeilly 2004). Siddiqui et al. (2012) reported that exogenous S supply in combination with N can alleviate the negative effects of salt stress in *B. juncea.* It was observed that decrease in nitrate reductase activity, N content, growth, and photosynthetic activity under salinity was restored with soil application of N and S at the rate of 100 mg kg^{-1} soil. Moreover, combined application of N and S resulted in better growth and proline accumulation compared to individual application of these nutrients.

Exposure to HMs not only poses serious threat to productivity of food crops but also threatens the safety of human nutrition. S nutrition helps to reduce toxic effects of metal elements in *Brassica* species. For example, Bashir et al. (2015) suggested that S pool is needed to synthesize GSH, PCs, and non-protein thiols to alleviate Cd toxicity in *B juncea*. They found that S-deficient plants exhibited higher oxidative activity under Cd stress. Contrarily, S application markedly enhanced CAT, APX, and GR activities to alleviate Cd-induced oxidative stress in *B. juncea*. Similarly, Zhong et al. (2012) found that S-treated *B. napus* plants exhibited lower As content in roots and grain compared to S-deficient plants. They were of the view phytoremediation capacity of rapeseed could be increased by S fertilization.

14.4.3 Soybean

The production of soybean is threatened by climatic change with more frequent occurrence of drought stress around the globe (Dai 2013; Foyer et al. 2016). Studies conducted under field and controlled conditions have shown that water stress can cause 25–50% yield reductions in soybeans (Frederick et al. 2001; Sadeghipour and Abbasi 2012). It has been well documented that S nutrition plays a significant role against drought stress in crop plants. Its metabolite GSH has been reported to scavenge reactive oxygen species (Astolfi et al. 2012). Exogenous H_2S application increased the biomass and survival of soybean plants grown under terminal drought stress (Zhang et al. 2010). Water deficit conditions drastically decreased the chlorophyll contents and antioxidant activity of soybean seedlings. Foliar application of H_2S significantly improved the antioxidant activity and chlorophyll contents of seedlings. Moreover, delay in the accumulation of hydrogen peroxide, superoxide anion, and malondialdehyde was also observed in plants sprayed with H_2S compared to control. Cigelske (2017) investigated the combined effects of N and S on soybean. It was reported that application of N significantly improved the vigor and yield but decreased the nodulation in soybean plants. However, S application decreased protein content but significantly increased nodulation in rhizosphere. Seed priming with sole and mixed solutions of $ZnSO_4$ and $FeSO_4$ alleviated the detrimental effects of drought stress in soybean at reproductive stage (Dehnavi and Sheshbahre 2017). They found a significant increment in photosynthetic rate, transpiration rate, stomatal conductance, and photosynthetic characteristics of plants raised from nutrient-primed seeds compared to hydropriming. Similarly, Heidarzade et al. (2016) reported that $FeSO_4$ application in combination with molybdenum markedly enhanced the yield attributes of soybean under drought stress. Comparative effects of KCl and K_2SO_4 application on physiological activities of soybean seedlings exposed to salt stress were investigated by Adhikari et al. (2019). They found that application of K_2SO_4 at 2.5% was more effective than KCl to improve growth, flavonoids, total phenols, antioxidant activity, carotenoids, and chlorophyll contents of salt-stressed soybean seedlings.

14.5 Conclusion

Considering the importance of S-containing metabolites in improving abiotic stress tolerance in plants, the application of S-containing fertilizers has become imperative to improve yield and quality of food crops in recent past. Low S availability severely hampers uptake, distribution, and assimilation of plant nutrients such as N, P, K, Zn, B, and Ca. Moreover, plants grown in S-deficient soils exhibit high susceptibility to environmental stresses like drought, salinity, and metal ions. Despite extensive research on S metabolism and assimilation in crop plants in recent years, there are still many questions answered. Future studies focused on increasing our understanding about specific gene expression in response to S application would help us to develop crop species tolerant to a wide array of environmental extremities. Studies triggered to boost our knowledge about interactive pathways of S assimilation and phytohormones regulation are of particular importance in this regard.

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