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Sulfur Nutrition in Plant Growth Promotion by Sulfur Oxidizing Bacteria: A Review

K. Sowmya[1], S.L. Sivapriya[2]

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ABSTRACT

Since sulfur is a vital nutrient for plant development, a lack of sulfur can result in significant reductions in crop yield. Sulfur deficiency often results in the addition of sulfur fertilizers to soil, typically in reduced forms like elemental sulfur. However, the reduced sulfur fertilizers must be converted to sulfate by microbes before they can be utilized by plants. The purpose of this review article is to explore the natural occurrence of sulfur in soil, the overall conversions that sulfur undergoes, its function in plant physiology, the variety and microbial oxidation of different reduced sulfur forms, it can boost plant growth by measuring sulfur oxidation in soil and modifying factors that influence sulfur oxidation.

Key words: Elemental sulfur, Plant growth, Sulfur bacteria, Sulfur oxidation.

[1]Department of Agricultural Microbiology, School of Agricultural Sciences, Bharath Institute of Higher Education and Research, Tambaram, Chennai-600 001, Tamil Nadu, India.
[2]Department of Science, Janani Public School, Bangalore-560 001, Karnataka, India.

Corresponding Author: K. Sowmya, Department of Agricultural Microbiology, School of Agricultural Sciences, Bharath Institute of Higher Education and Research, Tambaram, Chennai-600 001, Tamil Nadu, India. Email: ksowmyatnau@gmail.com

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Besides nitrogen, phosphorus and potassium, sulfur (S) is becoming recognized as an essential nutrient for plants. All compounds containing reduced sulfur are composed of cysteine and methionine, which form the building blocks of cysteine and methionine (Sharma *et al*., 2022). Sulfur is crucial for the survival of both plants and animals. The first documented case of sulfur deficiency was reported in 1933, despite being essential to plants in quantities like phosphorus. The initial observation of sulfur deficiency in wetland rice occurred in 1938. Both dryland crops and wetland rice have been identified as being negatively affected by sulfur deficiency over the past decade. Tropical regions are notorious for sulfur deficiencies arising in different types of andosols, vertisols, alfisols, ultisols and oxysols. Sulfur deficiency has been documented in wetland rice from Bangladesh, Burma, India, Indonesia, Japan, the Philippines and Sri Lanka. Reports indicate that 23 different crops in 40 tropical nations have shown positive responses to sulfur. Low sulfur fertilizer applications have increased, organic manure use has fallen, intensive cropping practices have declined and atmospheric pollution has decreased (Camberato and Casteel, 2017). Sulfur fertilizers, typically in reduced form like elemental sulfur, are used to resolve sulfur deficiencies in soils. The application of sulfur oxidizers accelerates the natural oxidation process of sulfur and hastens the production of sulfates, thus making them accessible to plants during crucial growth phases, which ultimately leads to higher crop yields (Valle *et al.,* 2019; Skwierawska *et al.,* 2016; Anandham *et al.,* 2007; 2008a; Stamford *et al.,* 2013; Stamford *et al.,* 2015). A variety of microorganisms, including prokaryotes and green sulfur bacteria, have been identified that either obligately or facultatively use sulfur compounds as electron donors and oxidize these compounds into sulfate. Sulfur oxidizing bacteria such as *Thiooxidans, Pseudaminobacter salicylatoxidans* and *Paracoccus* are recommended as inoculants for different rice-growing ecosystems. Therefore, this study has isolated microorganisms from several ecological environments, but currently, there is no appropriate sulfur bio-inoculant available (Rameez *et al.*, 2021). This review article discusses the natural occurrence of sulfur in soil, the general transformations of S, the physiological role of sulfur in plants, the diversity and microbiological oxidation of various forms of reduced S, methodologies for quantifying sulfur oxidation in soil, factors that influence S oxidation in soil and the implications of using sulfur-oxidizing bacteria (SOB) as plant growth promoters in the agro-ecosystem.

Sulfur in soil

Among the 105 elements that compose the Earth's crust, sulfur is found in a concentration of approximately 0.03%, ranking as the 17th most prevalent element. The elemental sulfur found in soil is primarily the mineral sulfides, sulfates, hydrogen sulfides and organic sulfur compounds. Minerals such as pyrite (FeS_2) provide most of the sulfur in soils. Soil redox potential is closely linked to the oxidation state of sulfur in pyrite during weathering and soil formation. Reactions involving the oxidation and reduction of sulfur

occur quite readily, leading to a wide variety of reactions that sulfur experiences in the soil. Soil sulfur content is generally influenced by three factors: (1) organic matter, (2) clay percentages and clay minerals, (3) levels of iron and aluminum oxides.

The organic sulfur content in soil rises with increased humus levels. Peat and marsh soils have a high concentration of organic sulfur. In the South Pacific, the total sulfur content tends to be lower in soils with minimal organic matter (Germida *et al.,* 2021). Organic matter and sulfur deficiency are common in tropical soils due to weathering and leaching. In southern China, there is a positive correlation between total sulfur and the percentage of clay. Soils with iron and aluminum oxides retain sulfur longer than those with coarse textures, partly because they contain more organic matter (Das *et al*., 2022).

Fractions of soil sulfur

Plant availability of sulfur(S) is not directly related to soil sulfur(S) levels. In soil, sulfur exists in several forms, so its availability to plants depends on how it is transformed and how it interacts with other sulfur fractions (Fig 1) (Germida *et al.,* 2021).

Organic sulfur compounds

Like organic matter, organic sulfur(S) has a decreasing distribution in soil profiles as depth increases. There are three kinds of soil organic S: cation -bonded sulfide, non - cation- bonded sulfide and humus sulfide. Generally, humid and semiarid soils have large amounts of C-bonded organic S. Isolating this fraction is challenging due to the significant transformations that S-containing compounds undergo. In soil, trace amounts of sulfur can be found despite the fact that sulfur is only found in small amounts in amino acids (Kodavali and Khurana, 2022).

Sulfate polysaccharides, like non-carbon-bonded sulfur, are thought to be present in many forms, including unidentified ester sulfates. A small portion of organic sulfur is found within soil biomass. However, the sulfur content in microbial tissue is highly reactive and plays a key role in the turnover of sulfur, impacting its availability to plants (Stellhorn *et al.,* 2022; Ranadev *et al.,* 2023).

Inorganic S

In soil, inorganic sulfur predominantly exists as sulfate. When oxygen is lacking, sulfur appears as its reduced form. Plants obtain sulfur through the soil's liquid phase. A significant portion of sulfur in calcareous and saline soils is found as gypsum ($CaSO_4 \cdot 2H_2O$). The solid phase of sulfur consists of sulfate retained in an adsorbed state in arid areas, such as $CaSO_4$, $MgSO_4$ and Na_2SO_4. Iron oxide and aluminum oxide can adhere to sulfate. This sorption primarily occurs through ion exchange facilitated by the charges present on clay minerals and oxides, with the

Table 1: Inorganic forms of sulfur in soil (Bouranis 2020).

Oxidation state	Sulfur state	Molecular formula
-2	Sulfide	S^{2-}
-2	Hydrogen sulfide	H_2S
-2, 0	Pyrite	FeS_2
0	Elemental sulfur	S^0
-1, +5	Thiosulfate	$S_2O_3^{2-}$
+4	Sulfite	SO_3^{2-}
+6	Sulfate	SO_4^{2-}
+6	Sulfuric acid	H_2SO_4
+3	Hyposulfite (dithionite)	$S_2O_4^{2-}$
+4	Dithionate	$S_2O_6^{2-}$
-2, +6	Trithionate	$S_3O_6^{2-}$
-2, +6	Tetrathionate	$S_4O_6^{2-}$
-2, +6	Pentathionate	$S_5O_6^{2-}$

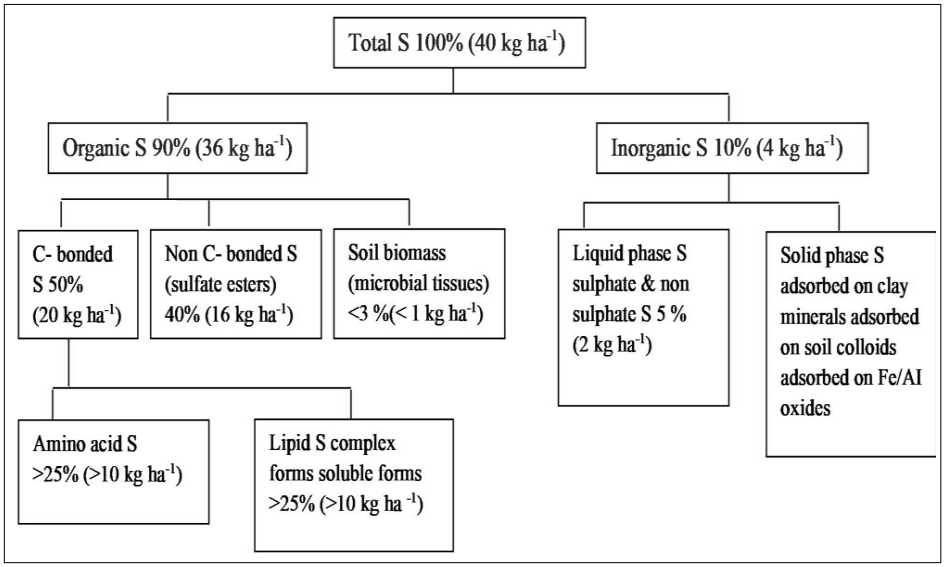


Fig 1: General distribution of various sulfur fractions present in soils (Germida *et al.,* 2021).

process becoming more pronounced as soil pH decreases (Table 1) (Narayan *et al.,* 2023).

Plant sulfur and Its physiological role

Sulfur compounds have a wide range of physiological functions. Two perspectives can be taken when looking at sulfur's function: Directly within compounds and indirectly at the level of influencing nutrient synthesis. APS (adenosine - 5′ phosphosulfate) and PAPS (3′-phosphoad-enosine - 5′ phosphosulfate) are two of the primary sources of sulfur for crop plants. Sulfate serves as the main source of sulfur for crop plants (Fujita and Uesaka, 2022). This strongly implies that sulfur plays a role in the synthesis of chlorophyll. Ferredoxin is categorized as an iron-sulfur enzyme, which lacks a cofactor but typically has equal amounts of iron and sulfur atoms in a specific unstable form that can break down in the presence of acid. In the reduction of nitrogen, NADPH passes on reducing equivalents to ferredoxin, an iron-sulfur protein. Further studies have demonstrated sulfur's role in the TCA cycle and glycolysis (Tabak *et al.,* 2020).

Sulfur has also been recognized as an essential factor in the synthesis of flavonoids and carotenoids. Additionally, sulfur is crucial for the synthesis of polyamines. The biochemical roles of naturally occurring polyamines include regulating the physical and chemical characteristics of membranes, influencing the structure and function of nucleic acids, modulating enzyme activities and overseeing molecular synthesis (Slocum and Flores, 2024).

Isothiocyanates possess antibacterial and antifungal characteristics as well. *Brassica* species can prevent the infection of the mildew pathogen *Peronospora parasitica* through the enzyme-mediated production of allyliso thiocyanate from sinigrin following tissue injury (Velu *et al.,* 2018). In pea plants, a reduced level of sulfur nutrition led to decreased levels of nitrogen, silicon, iron, calcium, magnesium, sulfur and crude ash content, while phosphorus and aluminum contents in both shoot and root tissues increased (Shah *et al.*, 2022). When sulfur and zinc are applied, the presence of one nutrient tends to lower the concentration of the other in the shoots. The interaction between sulfur and zinc likely occurs at absorption sites as well as within the plants themselves (Noman *et al.,* 2020).

Allylisothiocyanate is the sharp and pungent compound found in mustard, which people consume in small quantities as a condiment. This isothiocyanate also serves as the primary flavor component in cabbage and other cruciferous vegetables (Harborne, 2014). Typically, local varieties of horseradish, both wild and cultivated, tend to be more pungent than imported types. Increasing sulfur levels led to a rise in allylisothiocyanate during decay, thereby enhancing its pungency. The allylsulfide content of Korean soil was positively correlated with sulfur availability (r=0.723, n=15, p=0.01) (Park *et al.,* 2024).

Sulfur effects on crops

The growth of legume plants is adversely affected when soil levels of phosphorus and sulfur fall below critical threshold levels (Chaudhary *et al.,* 2022). Compared to controls, elemental sulfur increased groundnut oil content by 5%, nodule biomass, pod yield, shoot length and dry matter while reducing chlorosis (Noman *et al.,* 2020; Balagangathar *et al.*, 2024). Sulfur increased the rate at which carbohydrates were converted into oil, resulting in more oil and yield per molecule (Singh *et al.*, 2010). The oil content of sesame increased by 3.2% with a sulfur application of 50 kg per hectare (Assefa *et al.,* 2021). Adding sulfur to mustard increased its oil content and seed yield (Sharma *et al.,* 2022). Soybean leaf area, dry biomass, pod count and 100 seed weight were improved with an application of 30 kg sulfur per hectare (Khan *et al.,* 2020). Wheat yield increases by 2.19 quintals per hectare due to an increase of 30 kg S per hectare, as well as an improvement of nitrogen, phosphorus and potassium absorption (Singh *et al*., 2020). Blackgram yield-related traits and overall yield were significantly enhanced by 30 kg of sulfur per hectare (Ramamoorthy and Ariraman, 2023). A micronized sulfur application increased wheat yield by 36% and sulfur uptake by 164%, according to Kulczycki, (2021). Rice, maize, field beans, wheat, cotton, sorghum and sunflower all grew better after sulfur application, according to Zenda *et al.* (2021).

Deficiency symptoms

Sulfur, which is a part of nitrate reductase, plays a crucial role in transforming nitrate into organic nitrogen. Therefore, a deficiency in sulfur disrupts nitrogen metabolism, accounting for the similarities in symptoms between sulfur and nitrogen deficiencies in various crops. Nevertheless, the symptoms are typically mild and not restricted to the older leaves. The appearance of sulfur deficiency is characterized by a light green hue affecting the entire plant. Legumes, particularly alfalfa, have a significant demand for sulfur, making them the first to exhibit signs of deficiency. In corn, sulfur deficiency can sometimes mimic other nutrient shortages like manganese or magnesium, leading to interveinal chlorosis; the upper leaves are often stripped, with veins appearing darker green than the surrounding tissues. To correct sulfur deficiency in crops, the application of sulfur-containing fertilizers is generally recommended (Table 2) (Bouranis, 2020).

Interaction between S and other nutrients in soil

The presence of anions like sulfate (SO_4) in the soil solution relies on having equivalent amounts of counter cations such as calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^{+}) and potassium (K^{+}). Consequently, the availability of sulfate is influenced by the concentration of these cations within the soil solution. During the oxidation of reduced sulfur species to sulfate, hydrogen ions are released, which can displace other cations from soil colloids through exchange

processes. These cations may help maintain the balance of sulfate in the soil solution. However, cations such as calcium (Ca^{2+}) can limit sulfate availability by forming insoluble compounds like calcium sulfate ($CaSO_4$). When calcium carbonate ($CaCO_3$) is added, it can result in higher levels of soluble sulfate. This effect may be attributed to the release of adsorbed sulfate due to an increase in soil pH (Anandham *et al.,* 2011).

Sulfur oxidizing bacteria

Different microorganisms, including prokaryotes and green sulfur bacteria, have been identified that use sulfur compounds as electron donors, either obligately or facultatively and convert them to sulfate (Rana *et al.,* 2020). Alpha-, Beta- and Gammaproteobacteria are the prokaryotes that oxidize sulfur. In addition to chemolithotrophs and photolithotrophs, mixotrophs, photoheterotrophs and heterotrophs can be classified into these prokaryotes based on their physiological characteristics. A chemolithotroph, or chemosynthetic autotroph, includes members from bacteria and Archaea. All three categories include some important organisms in geomicrobiology (Zhao *et al.,* 2022). These microorganisms obtain energy for their metabolic processes from the oxidation of inorganic substances and incorporate carbon as CO_2, HCO^{3-}, or CO (Kazemi *et al*., 2021). Bacteria are known to be photolithotrophs, but Archaea are not known to be photolithotrophs. The photosynthesis process converts sunlight into chemical energy, which is used by these microorganisms to perform metabolic activities and encapsulates carbon as CO_2, HCO_3, or CO_3 (Dahl 2020; Nosalova *et al*., 2023). There are some microorganisms that produce oxygen as a byproduct of photosynthesis, while there are others that cannot release oxygen during photosynthesis (Khasimov *et al.,* 2021). Photoheterotrophs are primarily found among bacteria, although a few Archaea, like extreme halophiles, are also included. Heterotrophs include both bacteria and archaea, which get energy from sunlight but get carbon from organic carbon. The organisms oxidize organic compounds for energy and

Table 2: Fertilizer sources of sulfur.

Name of fertilizer	Chemical formula	Analysis N-P_2O_5-K_2O (%)	Sulfur (%)
Highly soluble			
Ammonium sulfate	$(NH_4)_2SO_4$	21-0-0	24
Ammonium thiosulfate (60% aqueous solution)	$(NH_4)_2S_2O_3$	12-0-0	26
Magnesium sulfate	$MgSO_4.7H_2O$ (Epsom salt)	0-0-0	14
Superphosphate	$Ca(H_2PO_4)_2 + CaSO_4$	0-20-0	14
Potassium magnesium sulfate	$K_2SO_4.2\,MgSO_4$	0-0-22	23
Potassium sulfate	K_2SO_4	0-0-50	18
Least soluble			
Calcium sulfate	$CaSO_4.2H_2O$	0-0-0	17
Insoluble			
Elemental sulfur	S	0-0-0	88-98

Table 3: Some of aerobic sulfur oxidizing bacteria (Zhang *et al*., 2025).

Autotrophic	Mixotrophic	Heterotrophic
Thiobacillus thioparus	*Thiobacillus intermedius*	*Thiomonas perometabolis (Thiobacillus)*
Halothiobacillus neapolitanus (Thiobacillus neapolitanus)	*Paraccus versutus (Thiobacillus versutus[d])*	*Beggiatoa spp.*
Thermithiobacillus tepidarius (Thiobacillus tepidarius)	*Thiobacillus organoparus*	
Acidithiobacillus caldus (Thiobacillus caldus)	*Pseudomonas spp.*	
Thiobacillus denitrificans[a]		
Thiobacillus thermophilica[b]		
Sulfobacillus thermosulfidooxidans		
Acidithiobacillus thiooxidans (Thiobacillus thiooxidans)		
Acidithiobacillus albertensis (Thiobacillus albertis)		

[a]– Facultative anaerobe; [b]– Facultative autotroph; [c]– Archea; [d]– Can also grow autotrophically and heterotrophically. Names in parenthesis are old name of respective bacteria.

assimilate organic compounds for carbon. They can either respire (oxidizing their energy source) through anaerobic processes or ferment their energy source *via* disproportionate (Dahl, 2020). Mixotrophs consist of certain bacteria and Archaea. They can simultaneously derive energy from the oxidation of reduced carbon compounds and oxidizable inorganic compounds and may obtain carbon from both organic sources and CO_2 at the same time, or they may completely derive energy from oxidizing an inorganic compound while sourcing their carbon from organic compounds (Table 3 and 4).

Sulfur-oxidizing bacteria may benefit from mixotrophic metabolism. Sulfur-oxidizing bacteria may benefit from co-oxidization of sulfur compounds along with organic substrates because low levels of sulfur compounds might inhibit growth (Nyamath *et al.*, 2024). When grown in a mixotrophic medium containing glucose/glutamate/acetate and thiosulfate, *Starkeya novella* and *Thioclava pacifica* oxidized thiosulfate and increased growth. Several studies have found that bacteria can develop in environments that contain glucose and organic materials that contain thiosulfate, in which case the organic material influences thiosulfate oxidation in Thiovirga in *T. intermedius* and *Thiovirga sulfuroxydans* (Yousuf *et al.,* 2014). Conversely, thiosulfate has been found to hinder glucose uptake by impacting the enzymes involved in the glucose metabolic pathways, specifically the Entner-Doudoroff and pentose phosphate pathways in *T. intermedius, Starkeya novella* and *Paracoccus versutus* (formerly *Thiobacillus* A2) (Kumar *et al*. 2020; Anandham *et al.,* 2011). Anandham *et al.,* (2009a, b) discovered a mixotrophic metabolism utilizing thiosulfate/succinate or acetate in *Methylobacterium oryzae, Methylobacterium fujisawaense, Methylobacterium goesingense* and *Burkholderia kururiensis* subsp. *thiooxydans.*

Isolation and characterization of sulfur oxidizing bacteria

In 1904, Beijerinck successfully isolated thiosulfate-oxidizing bacteria (*Thiobacillus thioparus*) from both freshwater canal sediment and saltwater environments. He also noted the formation of a dense pellicle made of sulfur that enveloped the bacterial cells produced by *T. thioparus*. This organism has been extracted from a variety of sources including soil, ditch water, sewage and seawater, with its ability to oxidize sulfur and sulfide being examined by numerous researchers. Bounaga *et al.* (2022) isolated a microorganism that could quickly oxidize sulfur into sulfuric acid. This organism was characterized as a small, colorless, non-filamentous type that primarily utilized elemental sulfur for energy, without accumulating sulfur inside or outside its cells. In certain instances, sulfur formed a layer on the surface of the liquid or adhered to the walls of the flasks, while in other cultures, delicate membranes devoid of sulfur surfaced at the top. Some cultures exhibited a combination of these phenomena.

Table 4: Some anaerobic sulfur oxidizing bacteria (Zhang *et al.,* 2025).

Photolithotrophs	Chemolithotrophs
Chromatium spp.	*Thermothrix thiopara*[a,b]
Chlorobium spp.	*Thiobacillus denitrificans*[b]
Ectothiorhodospira spp.	
Rhodopseudomonas spp.[a]	
Chloroflexus aurantiacusa[b]	
Oscillatoria sp.[b]	
Lyngbya spp.[b]	
Aphanothece[b]	
Microcoleus spp.[b]	
Phormidium spp.[b]	

[a]– Facultative autotroph; [b]– Facultative anaerobe.

Anandham *et al.* (2011) obtained sulfur-oxidizing bacteria from their natural environment by utilizing mineral media that contained either elemental sulfur or thiosulfate as an energy source. It is possible to selectively differentiate neutrophilic from acidophilic species with the use of pH-varying media. Employing an acid ferrous sulfate medium often promotes the selection of *A. ferrooxidans*, while an anaerobic thiosulfate medium (pH 7) enriched with nitrate is particularly effective in isolating *T. denitrificans* and *Acidiphilium acidophilum* (formerly known as *Thiobacillus acidophilus*), which was initially found as a commensal of *A. ferrooxidans*. Nosalova *et al.* (2023) developed an enhanced medium that used gel rite as a gel for the isolation and counting of acidophilic chemolithotrophic *Thiobacillus* strains. Robust and well-defined dark brown circular colonies appeared on this medium within 48 hours. A spring water sample contained strains that are like *Sulfolobus* and *Thermus*, as well as thiosulfate-oxidizing microorganisms (Dahl, 2020). PH levels of approximately 4-6, temperatures of 40°C and yeast extract concentrations of 60 mg per 100 ml were identified as optimal conditions for thiosulfate oxidation (Kumar *et al.,* 2020). The extraction of *A. thiooxidans* from the Yugama Crater Lake in Japan and examined its impact on the sulfate budget. Thiosulfate-oxidizing, base-producing organisms like *Pseudomonas stulzeri, Pseudoaltermonas and Halomonas deleya* were obtained from the marine and hydrothermal vents of New England (He *et al.*, 2022). Oligonucleotide probes were created to detect *Thiobacillus* and *Acidiphilium* in environmental samples (Anandham *et al*., 2011). Wen *et al.* (2012) successfully isolated *Acidithiobacillus* from sewage sludge by utilizing a modified Waksman medium.

Recent studies have demonstrated that sulfur-oxidizing bacteria can survive in extremely alkaline and saline conditions. An abundance of obligate autotrophs has been found in saline, alkaline lakes in Central Asia, Africa and North America, which exist in relatively significant numbers under these extreme conditions. In the presence of sodium carbonate/bicarbonate-buffering media, all strains demonstrated excellence at a pH around 10; however, at pH lower than 7.5 and sodium concentrations below 0.2 M, they are not able to grow. Phylogenetic and physiological differences among the isolates led to the identification of

two new Gammaproteobacteria genera: *Thioalkalimicrobium* and *Thioalkalivibrio*. One of three species in *Thioalkalispira* is obligately microaerophilic, *Thioalkalispira microaerophila*. (Kong *et al.*, 2022). Recently, Anandham *et al.,* (2005; 2007; 2008a, b; 2009a, b; 2010) have reported the isolation of numerous obligate and facultative chemolithotrophic thiosulfate-oxidizing bacteria from rhizosphere soils, noting their widespread occurrence in the rhizospheres of crop plants in Korea.

Mass multiplication that oxidize sulfur

Ensuring cell survival and functionality in both rhizosphere and non-rhizosphere soils is crucial for the effectiveness of any inoculation approach. To improve the introduction of large microbial populations and enhance their preservation in soil, inoculum formulations utilizing carrier materials have been implemented. The inoculant serves as the vehicle for transporting bacteria from the production site to the living plant, while the carrier is viewed as the means of delivering live microorganisms from the production facility to the agricultural field; however, there is currently no universal carrier or formulation available for effectively releasing microorganisms into the soil. Anandham *et al.,* (2005; 2007) developed a pellet formulation for sulfur-oxidizing bacteria.

Role of sulfur bacteria in sulfur nutrition

As a result, almost all sulfur present in soil environments (over 95% of total sulfur) cannot be directly absorbed by plants. Organic matter contains around 95% of the total sulfur content of the soil. Breakdown or decomposition of organic matter results in mineralization of organic sulfur into the SO_4^{2-}, which will be available to plants (Blum *et al.,* 2013). Sulfate is produced more quickly by using sulfur-oxidizing bacteria. In recent years, sulfur-oxidizing bacteria have become increasingly popular as growth promoters that improve plant yields during critical growth phases. Groundnut nodules were increased by 32 per cent and nodule dry weight was increased by 43 per cent, respectively, when *Thiobacillus* sp. was introduced 60 kg per hectare (Table 3) (Anandham *et al*., 2007). When sulfur and *Acidithiobacillus* were applied along with phosphate and potash rocks, sugarcane stalk dry matter yield was significantly enhanced (Stamford *et al.,* 2015).

Factors influencing SOB in Farming system

Soil temperature

Temperature greatly influences sulfur mineralization in soil. A temperature below 10°C and a temperature exceeding 40°C significantly reduce the rate of sulfur mineralization, whereas around 30°C is the optimal temperature. In multiple studies, sulfur oxidation rates have been shown to increase as soil incubation temperatures rise. For example, sulfur oxidation rates after 57 days of incubation were 8% at 5°C, 22% at 15°C and 47% at 30°C (Watling *et al.,* 2016).

Soil pH

pH plays a major role in the bio-oxidation of sulfur in the soil. If the soil pH is between 6.5 and 6.0, sulfur oxidation rate increases, but when the pH decreases, sulfur oxidation rate decreases. Neutral *Thiobacillus* species and heterotrophs, which thrive in neutral to alkaline soil conditions, are common sulfur-oxidizing bacteria (SOBs). In the upper 30 cm of the soil profile, pH and electrical conductivity (EC) are negatively related to the plant-available sulfur, while in the lower 30-60 cm, they are positively related to organic carbon. (Kang *et al.,* 2021).

Soil moisture

Moisture and aeration, together with temperature and pH, are vital abiotic factors affecting sulfur oxidation in soils, showing a parabolic relationship where oxidation is minimal at low moisture, increases as moisture approaches an optimal level (around 60% of field capacity) and peaks before declining. Soil moisture is affected by factors like soil type, texture and aeration, with adequate aeration being vital for the growth of sulfur-oxidizing bacteria, as poor aeration can impair their development and reduce sulfur oxidation rates (Pourbabaee *et al.,* 2020).

Land cultivation and agronomic practices

Conventional tillage can lead to a swift reduction in soil organic matter, resulting in decreased sulfur levels and diminished long-term fertility of the soil. Soils that are regularly treated with Sulfur show a higher count of *Thiobacillus* spp., which suggests a greater potential for Sulfur oxidation compared to soils that have never been treated with Sulfur, indicating a priming effect from the oxidation by Thiobacillus spp. This type of soil also influences the rate of sulfur oxidation. Typically, sulfur oxidation occurs at a higher rate in sandy loam, followed by clay soil, while it is significantly lower in silty clay soil (Malik *et al.,* 2021).

Crop and cropping system

As demonstrated in fallow fields, the type of crop and cropping system plays a significant role in influencing sulfur transformations within the soil, primarily because of the heightened microbial biomass present in the rhizosphere. Implementing cropping techniques that minimize nutrient loss and enhance soil organic matter could be beneficial for increasing the availability of sulfur in the soil during years conducive to mineralization, all while reducing the dependency on added fertilizer sulfur (Iannucci *et al.,* 2021).

Soil microbes

Soil microorganisms play a crucial role in transforming reduced sulfur compounds in the soil into a form that can be absorbed (SO_4^{2-}). While many microorganisms participate in sulfur oxidation, bacteria, particularly Thiobacillus and related species, have a significant effect

on this process (Rana *et al.,* 2020). The quantity and activity of microbial biomass affect the rate at which elemental sulfur is oxidized in agricultural soils. The oxidation of sulfur in soil is primarily carried out by heterotrophic sulfur-oxidizing groups, with autotrophic microorganisms following behind. A large proportion of organic sulfur in the soil exists as sulfate esters (up to 60%), which can be readily mineralized through the action of enzymes produced by a wide range of heterotrophic bacteria, including *Pseudomonas* and *Thiobacillus* species (Rana *et al.,* 2020). Certain microbial species or genera within a crop's rhizosphere have a more significant influence on sulfur cycling than others found in the crop itself. However, due to the fact that most soil microorganisms cannot be cultivated in artificial media, this functional specialization has been largely overlooked. As a result of this limitation, cultivation-based methods offer a distorted view of microbial ecology in the soil. To gain a better understanding of the involvement of soil microorganisms in sulfur cycling, a targeted investigation into functional diversity is necessary. This can be achieved through cultivation-independent techniques like stable isotope probing and soil genetic profiling (Alcolombri *et al.,* 2022; Dumont and Hernández García, 2019).

Particle size

Effective oxidation requires that *A. thiooxidans* come into direct contact with Sp particles (Ranadev *et al.,* 2023). To enhance the effectiveness of sulfur fertilizer (Sp), the particle size of applied sulfur should ideally fall between 80 and 1000 mesh or be even finer.

Soil organic matter

Organic carbon and soil organic matter have a significant positive relationship with soil sulfur. Organic sulfur comprises a varied array of soil microorganisms and partially decomposed remains of plants, animals and microbes, which accounts for about 95% of the total sulfur found in most agricultural soils (Kodavali and Khurana, 2022). Fresh organic sulfur decomposes more quickly than older organic sulfur, which is released at a slower rate. Organic materials such as wheat straw, broom grass clippings, farmyard manure, poultry litter and peat moss have been found to enhance soil sulfur levels (Lee *et al.*, 2021; Malik *et al.,* 2021).

Prospects for the future in Agriculture

The use of SOB extends beyond agriculture and encompasses a variety of other sectors. In environmental science, they are vital in neutralizing H_2S, remediating soil and treating wastewater. Furthermore, with the current focus on nanotechnology, SOB is employed in the creation of nanoscale sulfide particles that exhibit superior optical, electronic and mechanical attributes compared to other metal nanoparticles. Furthermore, SOB is crucial for increasing the operational lifespan of bio-electrochemical fuel cells, particularly sediment microbial fuel cells (SMFC), by reducing phosphorus discharge from the sediment, thereby supporting electrical current production. SOB thrives in extreme environmental settings, including high salinity regions (halophytes) and acidic soils (acidophilic), offering extensive genetic variation that can be utilized to tackle various challenges in agriculture and other scientific disciplines through biotechnological methods. Despite its potential, the low biomass of SOB, the acidification of the process solution and the selectivity of Bio-S^0 hinder its industrial use. Consequently, additional efforts must be made to enhance the BDS process for industrial purposes through various research avenues. In the energy field, researchers are utilizing cellulose nanofiber derived from SOB to enhance lithium-sulfur batteries (LSBs). In the field of metallurgy, the bioleaching of different metals, including Cu, Zn and Fe, using SOB proves to be cost-effective. At present, CRISPR-Cas is a widely used method for genome editing. This system can be employed to create genetically modified SOB with improved thermostability, solvent resistance and broader substrate specificity, facilitating better utilization of SOB in agriculture and other sectors.

CONCLUSION

A growing number of soils around the globe are experiencing sulfur deficiency, which can result in lower crop productivity and yield declines. In India, about 46% of soils lack adequate sulfur, causing crop yields to drop by 20% to 40%. Similar observations have been reported from various regions worldwide. Although sulfur exists primarily in organic forms in most soils, it is not easily accessible for plants to absorb. Utilizing S^0 presents a cost-effective option for swiftly restoring sulfur levels, but it requires oxidation to sulfate for plant uptake. The oxidation efficiency of S^0 in soil is affected by various soil and environmental factors, along with the particle size of sulfur and the diversity of soil microorganisms. The biotechnological use of sulfur-oxidizing bacteria (SOB) provides a chance to create innovative biofertilizers and enhance the sulfur oxidation process in soil. While there has been evidence of the positive impacts of sulfur combined with SOB on crop growth and yields, research in this area is still limited and the persistence of SOB in different formulations has not been investigated. Additionally, SOB has several traits that promote plant growth, such as the production of IAA, siderophores, antimicrobial substances and ACC deaminase activity, which can be utilized as beneficial properties in biofertilizers. Additional research is required to explore and examine the different biochemical pathways involved in sulfur oxidation across various soils in diverse agroclimatic regions.

Conflict of interest

The authors declare no commercial or financial conflict of interest.

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