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Understanding sulfur dynamics in soil ecosystems: applications of sulfur-oxidizing bacteria– a review

Hossein Besharati[1†], Maryam Samani[2] and Ahmad Asgharzadeh[1]

[1] *Agricultural Research, Education and Extension Organization, (AREEO), Soil and Water Research Institute, Karaj, Iran*
[2] *Department of Soil Science, University of Zanjan, Zanjan, Iran*

†*Corresponding Author Email: Besharati1350@yahoo.com*

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ABSTRACT

Sulfur (S) is an essential element for plants, playing a crucial role in various biochemical processes that are vital for their health.. Insufficient sulfur in the soil can profoundly affect plant health and crop yield. Agriculture commonly relies on sulfur fertilizers containing either sulfate or elemental sulfur (S^o) as a sulfur source. However, S^o, being more cost-effective and less prone to leaching than sulfate-(SO_4^{-2}) is favored, but, S^o must undergo oxidation to sulfate before plants can readily utilize it, a process largely facilitated by soil microorganisms. The environmental conditions affecting microorganism populations and activities significantly influence S^o oxidation. Sulfur-oxidizing bacteria (SOB) are instrumental in sulfur cycling within soil ecosystems, impacting their availability and transformation. This review delves into the intricate connections among S dynamics, SOB, soil improvement, and plant nutrition. It explores how plants obtain and employ S, stressing its significance in protein synthesis, enzyme activation, and secondary metabolites production. Additionally, the review scrutinizes SOB's role in mediating S oxidation, which influences soil pH, nutrient availability, and plant-microorganism interactions. Moreover, it discusses the potential of SOB as biofertilizers to enhance sulfur availability and bolster plant growth. Various strategies for leveraging the beneficial effects of SOB in sustainable agriculture are examined, such as microbial inoculation. The review also addresses the environmental implications of sulfur cycling, emphasizing the importance of maintaining balanced sulfur levels in soil ecosystems to mitigate environmental pollution and optimize agricultural productivity. In conclusion, this review offers valuable insights into the dynamic relationship between sulfur, SOB, soil fertility, and plant nutrition. It underscores the potential applications of this understanding in sustainable agriculture and ecosystem management, emphasizing the necessity of sulfur management for fostering agricultural productivity and environmental sustainability.

Keywords: Auxin, Nitrogen, Phosphate, Phycobili Protein, Siderophore.

1. Introduction

Sulfur (S) is an essential element for plants, particularly in oil plants, and it is the fourth most widely used element in plant nutrition, following nitrogen, phosphorus, and potassium. In nature, sulfur ranks sixth in abundance, but it is the fourth most required element by plants after the three primary elements. The concentration of sulfur in soil can vary widely, ranging from 0.002 to 5%, with an average range of 0.01 to 0.5% , Tisdale et al. (1993) reported that sandy soils typically have the lowest sulfur content, with levels around 20 mg kg^{-1}, while tidal regions where sulfides (S^{-2}) accumulate can have the highest sulfur content, reaching approximately 35 $mgkg^{-1}$. According to Tisdale et al. (1984), sulfur is the most commonly used and cost-effective material for soil acidification. Researchers have been interested in using sulfur to reduce alkaline pH, enhance nutrient uptake, provide sulfate (SO_4^{-2}) for plants, and manage certain diseases. In sustainable agriculture management, understanding the quantity and dynamics of sulfur in soils is crucial for ensuring an adequate supply of sulfur for plant growth. This involves studying the main microbial processes in soil related to sulfur immobilization, mineralization, oxidation, and reduction. By comprehending these processes, farmers and researchers can make informed decisions regarding sulfur application and optimize its availability for plant nutrition. In soils, sulfur exists in two forms: organic and inorganic. The majority of sulfur is mineralized in terrestrial ecosystems, while a smaller portion is found in humid ecosystems. Regions characterized by wet, semi-arid, temperate, and subtropical climates, along with well-drained soils rich in organic matter, typically have higher sulfur concentrations in their surface layers. In noncalcareous soils, approximately 90% of sulfur is present in organic matter (Malakooti & Rezaei, 2001). The ratio between organic and inorganic sulfur content can vary significantly and is influenced by factors such as pH, drainage conditions, organic matter content, mineral composition, and soil depth. The distribution of organic sulfur within the soil profile differs depending on soil type and depth. Generally, the sulfur content in deeper soil layers is lower compared to the surface horizons (Malakooti & Homaei, 2003). The presence of sulfur in soil is essential for various reasons. Sulfur is a constituent of certain amino acids, proteins, and vitamins, playing a crucial role in plant metabolic processes. It is involved in the synthesis of enzymes and chlorophyll, which are essential for photosynthesis. Sulfur also contributes to the formation of secondary metabolites, such as phytochemicals and defense compounds, that help plants resist diseases and pests. Sulfur availability in the soil directly affects plant health and growth. Sulfur deficiency can lead to reduced crop yield, delayed maturity, and poor-quality products. Understanding the distribution and dynamics of sulfur in soil is important for effective soil and nutrient management. By assessing sulfur levels and considering factors such as soil pH, drainage, and organic matter content, farmers and researchers can make informed decisions regarding sulfur fertilization and address any potential deficiencies. In calcareous and saline soils, the majority of sulfur exists in the form of gypsum ($CaSO_4 \cdot 2H_2O$) (Malakooti & Homaei, 2003). Metal sulfides (S^{-2}) found in plutonic rocks serve as the primary source of sulfur in the soil. Through the process of weathering, the sulfur within these rocks oxidizes and converts into sulfate. These sulfates can then form soluble or insoluble salts, which accumulate as sediment in arid and semi-arid areas. Alternatively, they can be absorbed by living organisms or reduced to sulfide or elemental sulfur under anaerobic conditions. Some of the released sulfate is also carried into the oceans through drainage. Ocean water typically contains 7.2 mg L^{-1} of sulfur, but in highly saline lakes, sulfur concentrations can reach as high as 60 g L^{-1} (Tisdale et al., 1993). Sulfur is an essential nutrient for plant growth and crop production. The concentration of sulfur in plant leaves is often two times higher than that of phosphorus, highlighting the relative importance of sulfur in comparison to phosphorus (Tandon, 1991). Sulfur plays a vital role in the production of proteins and oils within plants. Since plants can absorb sulfur in the form of sulfate ions, the effectiveness of sulfur supplementation relies on its conversion to sulfate through oxidation when applied to the soil.

Leguminous plants and oilseeds have a higher sulfur requirement compared to grains. Sulfur is also a component of nitrogen-fixing enzymes, so increased sulfur intake in these plants enhances biological nitrogen fixation and raises sulfur concentrations within them. This, in turn, leads to higher production of sulfur-containing amino acids and improves the percentage and quality of plant proteins. Additionally, sulfur increases the oil content in legumes and oilseeds. However, sulfur deficiency not only reduces the quantity and quality of oils and plant proteins but also results in the accumulation of nitrates in plants (Tisdale et al., 1993; Dubey and Billore, 1995).

1.1. Sources of sulfur in soil

Sources of sulfur in soil can be categorized into inorganic sulfur and organic sulfur. In most agricultural and mineral soils, the total sulfur concentrations in the top 15 cm typically range between 50 and 100 $mgkg^{-1}$ (Syers et al., 1987).

a) Inorganic sulfur

Constitutes a relatively small proportion of the total sulfur in soil, usually less than 5%. However, in agricultural soils, it may account for a higher proportion, up to 25% (Saggar et al., 1998). Inorganic sulfur can exist in various forms, including sulfate, sulfite, thiosulfite, tetrathionate, elemental sulfur, and sulfide. Among these forms, sulfate (SO_4^{-2}) is the dominant fraction in most agricultural soils due to its stability under aerobic conditions. Sulfate is readily available for plant uptake as it can be dissolved in the soil solution. It can also be adsorbed onto mineral surfaces or precipitated as gypsum in soils that contain gypsiferous minerals. Sulfate retention in the soil profile is influenced by processes such as adsorption, desorption, precipitation, oxidation, and reduction. Adsorption of sulfate can limit its movement in the soil solution (Narsh et al., 1987). In most soils with pH > 6, sulfate adsorption is weak (Curtin and Syers, 1990), but in soils with high oxide content and low pH, sulfate adsorption can be significant (Singh et al., 1980). Naturally, sulfur occurs as an element within various minerals such as iron pyrites, galena, gypsum, and epsom salts. These minerals can serve as sources of sulfur in the soil. Additionally, atmospheric deposition of sulfur-containing compounds, such as sulfur dioxide (SO_2) from industrial emissions or volcanic activity, can contribute to the sulfur content in the soil.

b) Organic sulfur

Organic sulfur which is derived from organic matter, is another important source of sulfur in soil. Organic sulfur compounds are formed through the decomposition of plant and animal residues. The release of sulfur from organic matter occurs as a result of microbial activity, including the mineralization of sulfur-containing organic compounds.

Understanding the different sources and forms of sulfur in soil is crucial for managing sulfur availability and ensuring optimal plant nutrition. Organic sulfur makes up more than 90% of the total sulfur in well-drained, non-calcareous soils. It exists as a mixture of soil organisms and decomposed residues from plants, animals, and microbes (Kertez and Mirleau, 2004). The concentration of organic sulfur in the soil is closely related to the carbon and nitrogen content of the soil (Solomon et al., 2011). Research indicates that the gross mineralization of sulfur is more closely related to reduced sulfur species (sulfur bound to carbon, C-bound S) than to oxidized sulfur species.. This indicates that C-bound sulfur is more prone to microbial breakdown than ester sulfate sulfur. Ester sulfate sulfur, along with soluble and adsorbable sulfate, is typically regarded as the plant-available organic sulfur

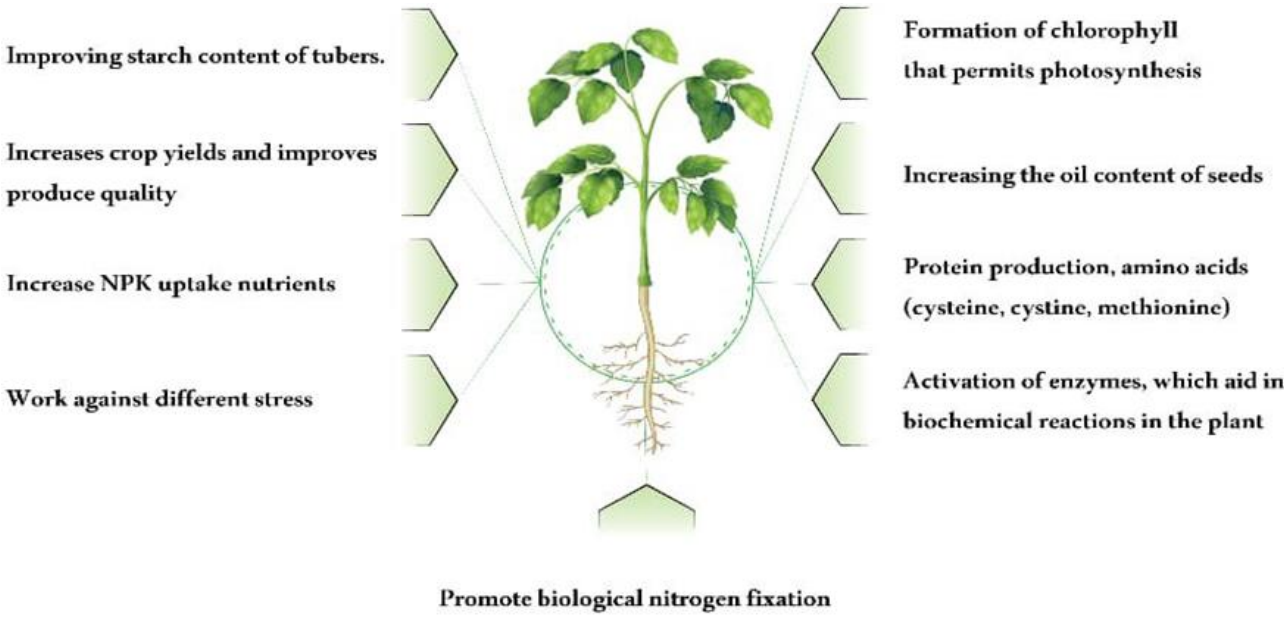

Fig 1. Schematic representation of sulfur functions in plants

in the soil. However, not all ester sulfate-S is readily available, and its availability can depend on its location within the structure of humic polymers (Lou and Warman, 1992). The dynamics and availability of organic sulfur in the soil are influenced by various factors, including the quality and composition of organic matter, microbial activity, and soil management practices. As organic matter decomposes, sulfur is released and can be transformed into different organic sulfur compounds. Microbes are essential for converting organic sulfur into mineral forms usable by plants. Understanding the role of organic sulfur and its interactions with organic matter and soil microorganisms is important for optimizing sulfur availability to plants and managing soil fertility. Soil management practices that enhance organic matter accumulation and microbial activity can contribute to facilitate the cycling and availability of organic sulfur in the soil..

1.2. The role of sulfur in plant growth and development

Sulfur is essential for plant growth, as reflected in various processes. Here are the key roles of sulfur in plant metabolism (Fig. 1):

a) **Protein Synthesis**: Sulfur is a crucial component of amino acids, including cysteine, cystine, and methionine, which are essential for protein synthesis. Proteins are involved in nearly all aspects of plant growth and development.
b) **Coenzyme and Vitamin Synthesis**: Sulfur is necessary for the coenzyme A synthesis, which is involved in several metabolic reactions. It is also a component of vitamins such as biotin and thiamine, which play important roles in plant metabolism.
c) **Chlorophyll Synthesis**: Sulfur is essential for the proper synthesis of chlorophyll, the pigment responsible for capturing light energy during photosynthesis. Adequate sulfur levels support healthy chlorophyll production and efficient photosynthetic activity.
d) **Volatile Oil Synthesis**: Certain plant families, such as Cruciferae (e.g., cabbage, mustard) and Liliaceae (e.g., onion, garlic), produce volatile oils. Sulfur is a key component of these oils, which contribute to the distinctive flavors and aromas of these plants.
e) **Biological Nitrogen Fixation**: Sulfur plays a role in biological nitrogen fixation in leguminous plants (e.g., clovers, peas, beans). It is involved in synthesizing enzymes and proteins necessary for converting atmospheric nitrogen into forms that plants can crops have varying sulfur requirements. Some crops, such as rapeseed, lucerne, and cruciferous forages, have high sulfur requirements. Others, like coconut, sugarcane, clover, grasses, coffee, and cotton, have moderate sulfur requirements. Crops such as sugar beet, cereal forages, cereal grains, and peanuts have low sulfur requirements (Spencer, 1975).

A sulfur deficiency can negatively impact plant metabolism, leading to reduced crop yields and lower quality produce. Sulfur deficiency affects fundamental metabolic processes, disrupting protein synthesis, chlorophyll formation, and other essential functions (Duke and Reisenauer, 1986). Therefore, maintaining adequate sulfur levels is crucial for promoting optimal plant growth, yield, and quality.

1.3. Deficiency symptoms and consequences in plants

Sulfur deficiency in plants can manifest through various visible symptoms. Here are the common deficiency symptoms associated with sulfur:

a) **Yellowing of Young Leaves**: Sulfur deficiency often leads to the yellowing of younger leaves due to reduced chlorophyll production. Since sulfur is not easily mobile within the plant, the deficiency symptoms primarily affect the newly formed leaves (Yoshida and Chaudhry, 1979).

b) **Pale Green Chlorosis**: Plants that are deficient in sulfur display a consistent pale green chlorosis across their tissues. The veins of the leaves may not retain a green color and can be even paler than the interveinal tissue. This symptom is especially noticeable in cultivars that do not have red pigmentation in their young leaves. (Chase and Widdowson, 1983).

c) **Stunted Growth and Reduced Tiller Number**: Sulfur deficiency can result in marked reductions in plant height and tiller (side shoot) number, particularly in cereal crops. The plants may fail to reach their normal size, and the activity of axillary buds, responsible for branching, is reduced

d) **Purple or Red-Brown Pigmentation**: In some cases, sulfur-deficient plants may develop purple or red-brown pigmentation on both young and old leaves. This pigmentation can appear on shoot tips, petioles (leaf stalks), and leaf margins. However, the presence of pigmentation can vary depending on the plant cultivar.

f) **Reduced Leaf Size and Branching**: Severe sulfur deficiency can cause reduced leaf size and stunting. The activity of axillary buds decreases further, resulting in fewer branches and a less bushy appearance Not all plants deficient in sulfur show visible symptoms, and significant growth reductions can happen without obvious indicators. Furthermore, symptoms can differ among various plant species and cultivars.(Blair et al., 1979; Islam and Ponnamaperuma, 1982).

1.4. Significance of understanding sulfur dynamics for agricultural productivity

Indeed, one of the significant properties of sulfur is its ability to exist in different oxidation states, ranging from -2 to +6. This property is crucial for the sulfur cycle in nature, which involves several stages: mineralization, immobilization, reclamation, and oxidation. In the atmosphere, sulfur is present in the forms of sulfur dioxide (SO_2) and hydrogen sulfide (H_2S). These forms of sulfur enter the atmosphere through natural processes like volcanic eruptions or human activities such as the combustion of fossil fuels. In the soil, sulfur can exist in various forms, including organic sulfur compounds, S^-, S, and SO_4^{2-}, which is the required form for plant uptake. Soil organic matter contains a significant portion of sulfur, but it is generally unavailable to plants. Over time, organic sulfur undergoes mineralization, a process in which it is converted into sulfate and becomes accessible to plants. Sulfur enters the soil through deposition from rainwater and the decomposition of plant and animal residues. It can also leave the soil through plant uptake, leaching (especially in sandy soils), and volatilization. Soil disturbance can increase the rate of sulfur volatilization. The movement of sulfur in the soil and its transformation from one form to another is similar to the nitrogen cycle. Sulfur availability to plants is closely linked to its cycling and transformations in the soil (Fig. 2).). In arid and semi-arid agricultural lands, Irrigation water is a considerable source of sulfate ions in soil.

1.5. Sulfur mineralization and immobilization

Immobilization of S involves the assimilation of sulfate by soil microorganisms , converting it to organic S. In contrast, mineralization is the process of converting organically bound sulfur back into inorganic sulfur, predominantly in the form of sulfate sulfur.(Schonenau and Malhi, 2008). Immobilization represents the incorporation of sulfate into ester sulfate-S and C-bounded S (Fitzgera et al., 1982). Sulfate can also be immobilized by microorganisms to become a component of microbial biomass and is used in the synthesis of microbial cell walls (Myanard et al., 1983). Sulfate immobilization can reduce the availability of sulfur (S) for plants, although can effectively reduce sulfate leaching (Zhao, 2015). On the other hand, mineralization of organic S leads to the release of plant-available sulfate-S. A model proposed by McGill and Cole (1981) describes the mineralization of organic S in soil, involving biochemical and biological processes. Biochemical mineralization involves the release of inorganic S from organic matter, driven by the sulfate demand of soil organisms. Biological mineralization, on the other hand, involves the conversion of C-bound S to inorganic S to meet the energy requirements of organisms in soils. The net mineralization of S from organic matter determines the change in sulfate-S concentration over time and plays a key role in the supply of sulfate for plant growth in unfertilized soils. In agricultural soils, the demand for sulfur (S) by crops often exceeds what can be provided through the mineralization of organic sulfur (Eriksen et al., 1995). Research has shown that net mineralization from farmyard manure and crop residues ranges from 3.5 to 5.6 mg of sulfur per kg of soil after 95 days of incubation (Boye et al., 2009). Additionally, studies found that mineralization from wheat straw and cabbage yielded 1.1 and 5.6 mg of sulfur per kg of soil, respectively, after 43 days of incubation.(Nziguheba et al., 2006).

1.6. Sulfur oxidation

Elemental sulfur oxidation is primarily carried out by soil microorganisms, making it highly influenced by factors

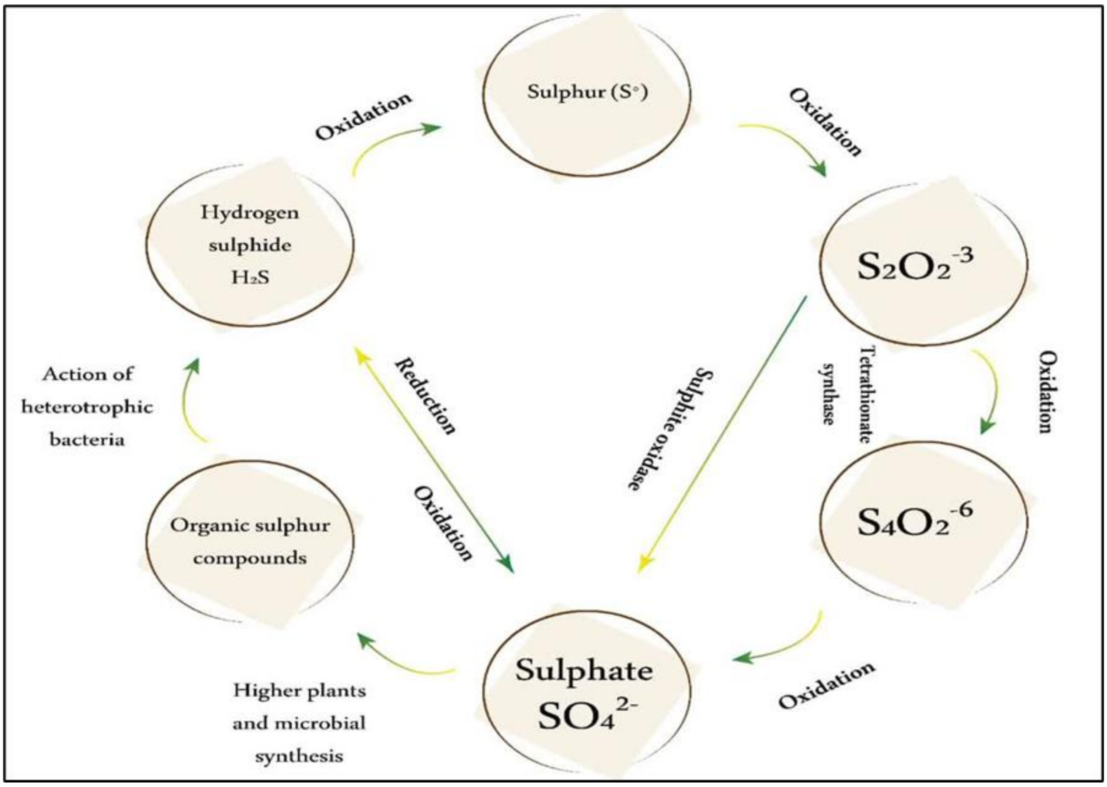

Figure 2. Sulfur cycle in soil. The sulfur cycle consists of four stages of mineralization, immobilization, reduction, and oxidation (Tabatabai ,1986)

that affect soil microbial activity and population. The oxidation of ES is known to be influenced by various environmental factors, such as temperature, water content, and aeration, as well as soil properties including soil texture, pH, and carbon content. Additionally, the particle size of ES has also been found to impact its oxidation process (Fig. 3). Detailed information regarding the effects of these factors on ES oxidation can be found in the comprehensive review by Gremida and Janzen (1993). They extensively examined the impact of environmental factors, soil properties, and ES particle size on ES oxidation. The oxidation of sulfur is influenced by several important factors, including:

a) Nutrient content in the soil (soil fertility level): Studies have demonstrated that when elemental sulfur is present in the soil and provided with suitable oxidation conditions, soil microorganisms, particularly *Thiobacillus* genus, consume significant amounts of sulfur during a crop season. This consumption leads to the oxidation of sulfur and the production of sulfuric acid, which subsequently reduces soil pH, increases nutrient concentrations in the soil, enhances nutrient absorption by plants, and ultimately promotes plant growth and yield (Khadem et al., 2015). SOM primarily require the same nutrients as plants, potentially with a few additional elements, and there is a continual competition between plants and microorganisms for the uptake of water and nutrients. Occasionally, the addition of sulfur to the soil and the increased activity of sulfur oxidizers, along with nitrogen consumption, may temporarily result in symptoms of nutrient deficiency in plants (Tisdale et al., 1984). Sulfur oxidation occurs more rapidly in soils enriched with phosphorus and potassium fertilizers compared to nutrient-poor soils. When sulfur is added to the soil with other fertilizers, its oxidation is accelerated compared to used alone. Research has shown that the presence of TSP (triple superphosphate) and ammonium phosphate fertilizers can enhance the oxidation of sulfur when consumed together. The beneficial effects of potassium, calcium, nitrogen, and phosphorus in fertilizers, the creation of favorable moisture conditions around fertilizers, the decrease in soil pH due to the dissolution of certain fertilizers, and the increased activity of acid-friendly oxidants have been linked to the increased sulfur oxidation observed (Deluca et al., 1989). SOM, particularly those from the *Thiobacillus* genus, have a high requirement for phosphorus. The presence of phosphorus fertilizers can enhance sulfur oxidation due to the increased activity of these microorganisms. Certain strains of sulfur-oxidizing microorganisms are even capable of tolerating heavy metals and can activate and oxidize sulfur in metal mines (Tisdale et al., 1984). Certainly, the amount of sulfur, the method of sulfur mixing with soil,

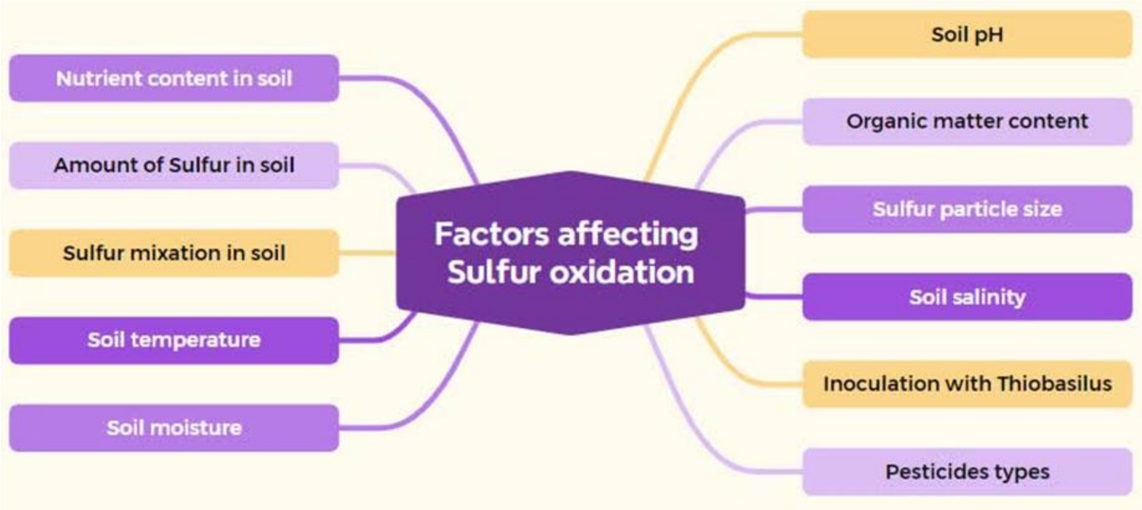

Figure 3. The most important factors affecting sulfur oxidation (Besharati, 2000)

temperature, soil ventilation, and moisture are additional factors that affect the oxidation of sulfur. Here's more information on these factors:

b) Amount of sulfur: Increasing the amount of consumed sulfur generally does not affect the percentage of sulfur oxidized, but it can increase the overall amount of oxidation to some extent. In certain cases, the slow oxidation of coarse sulfur particles can be compensated for by increasing the amount of sulfur consumption. Increasing the amount of sulfur enhances the exposure to sulfur-oxidizing microorganisms, resulting in increased sulfur oxidation. However, in soils with low buffering capacity, a rise in sulfur consumption may decrease the rate of sulfur oxidation.

c) Method of sulfur mixing with soil: The way sulfur is mixed with the soil significantly impacts the amount and rate of sulfur oxidation. Mixing sulfur with the soil is more effective than surface application or diffusion into the soil. When sulfur is uniformly mixed and distributed in the soil, several benefits arise:

- Increased availability of sulfur for sulfur-oxidizing microorganisms, allowing easy access to microorganisms in different parts of the soil;
- Improved moisture conditions for sulfur oxidation in the soil;
- Improved interaction between sulfur and soil particles reduces the negative effects of acidification caused by sulfur oxidation.

d) Temperature: Sulfur oxidation in soil is a biological process significantly influenced by temperature. As the temperature rises, up to a certain point, the activity of sulfur-oxidizing microorganisms also increases, leading to enhanced sulfur oxidation. This process occurs within a temperature range of 4 to 55 °C. At temperatures below 10 °C, sulfur oxidation happens slowly, while excessively high temperatures can kill sulfur-oxidizing microorganisms and stop sulfur oxidation altogether. The optimal temperature for sulfur oxidation in soil is generally around 25 to 30 °

b) Soil ventilation and moisture: Soil ventilation and moisture levels also impact sulfur oxidation. As soil moisture increases, sulfur oxidation tends to increase until it reaches an optimal level. However, further increases in moisture can reduce the oxidation rate due to oxygen depletion in soil pores. Sulfur oxidation decreases under moisture conditions below field capacity, as water availability becomes limited for sulfur-oxidizing microorganisms. The most suitable moisture range for sulfur oxidation is typically near field capacity (-0.59 bar). Sulfur oxidation is minimized at tentions of -0.1 to -1 MPa.

c) Soil pH: Sulfur oxidation is not limited by pH compared to nitrogen nitration. Sulfur oxidation can occur in soils with pH values ranging from 2 to 9 (Janzen and Bettany, 1987). Lime application to acidic soils can have varying effects on sulfur oxidation. Sometimes lime has no effect, while other times it increases oxidation, and in some cases, it reduces sulfur oxidation. Lime may increase oxidation by alleviating the toxic effects of elements like aluminum and manganese and by increasing calcium availability. On the other hand, negative effects of lime may be due to increased soil pH and a decrease in the number and activity of acidophilic bacteria. However, many studies have shown that lime application to acidic soils can increase sulfur oxidation (Stevenson, 1986).

e) Organic matter: Adding organic matter to soil enhances sulfur oxidation. Heterotrophic sulfur-oxidizing microorganisms use organic matter as a carbon and energy source, thus increasing their activity and the rate of sulfur oxidation. Organic matter improves soil physical properties (ventilation, permeability, moisture holding capacity) and chemical properties (cation exchange capacity, soil buffering properties), which further promote sulfur oxidation. The effect of organic matter on sulfur oxidation depends on the relative abundance of heterotrophic sulfur-oxidizing microorganisms compared to autotrophs. If heterotrophs are more abundant, organic matter addition has a greater impact on increasing sulfur oxidation due to the availability of organic substrates that support their growth and activity. In contrast, the population of autotrophs remains relatively unchanged. Besharati et al. (2000) found that sulfur had a significant positive effect on the population of autotrophic and heterotrophic sulfur-oxidizing bacteria in soil, but a negative effect on spore of *Bacillus* bacteria.

f) Sulfur particle size: The oxidation of sulfur particles is affected by their size. Smaller sulfur particles possess a greater specific surface area, facilitating direct contact with sulfur-oxidizing microorganisms and enhancing the rate of sulfur oxidation. The oxidation of sulfur particles increases significantly as their diameter decreases. This indicates that as the diameter decreases and the specific surface area increases, a greater amount of sulfur is oxidized.(McCaskill and Blair, 1987; Janzen and Bettany, 1987).

g) Soil salinity: Soil salinity reduces the rate of sulfur oxidation for two reasons. First, salinity increases the osmotic potential of water in the soil, limiting water availability for sulfur-oxidizing microorganisms. Second, the high concentration of ions in saline soils can have toxic effects on microorganisms, inhibiting their activity and negatively impacting sulfur oxidation (Besharati, 2000).

h) Pesticides: The effects of pesticides on sulfur oxidation vary depending on their chemical composition. Some pesticides contain sulfur and readily decompose in the soil, while others are toxic to sulfur-oxidizing microorganisms and are difficult to degrade (Besharati, 2000).

i) Inoculation of soil with *Thiobacillus*: *Thiobacillus* are the primary sulfur oxidizers in soil. Inoculating soil with these bacteria increases the rate of sulfur oxidation. Studies have shown that sulfur oxidation rates in *Thiobacillus-inoculated* soils can be about 11 times higher than in non-inoculated soils. In agricultural fields, sulfur-oxidizing microorganisms are present but in low numbers due to a scarcity of sulfur compounds. Therefore, the differences between inoculated and non-inoculated treatments may not be significant in some instances. (Tisdale et al., 1984). The presence of a sufficient population of sulfur-oxidizing microorganisms in the soil enhances sulfur oxidation, lowers local soil pH, increases nutrient solubility, and promotes plant growth.

Several studies have reported the involvement of both heterotrophic and autotrophic microorganisms in sulfur oxidation. Culture-based methods have provided insights into the role of these microorganisms, with some studies based on functional gene measurement showing the involvement of diverse bacterial groups in elemental sulfur oxidation (Anandham et al., 2008; Tourna et al., 2014; Xia et al., 2014). Autotrophic sulfur-oxidizing bacteria, such as *Thiobacillus* spp., are commonly found in soils, and their presence depends on soil properties and the addition of elemental sulfur. The number of *Thiobacillus* or *Thiobacillus*-like species increases with the enhancement of elemental sulfur application. Heterotrophic sulfur-oxidizing bacteria, on the other hand, are widespread in aerobic agricultural soils and show less variation compared to autotrophs during elemental sulfur oxidation (Lawrence and Geremida, 1988).

According to Janzen and Bettany (1987), sulfur oxidation is primarily influenced by the surface area of sulfur particles rather than their mass. This is because oxidation is a surface reaction, and only the sulfur atoms on the exterior surface are oxidized. Therefore, sulfur compounds with larger surface areas, including elemental sulfur, produce more SO_4^{2-} during oxidation compared to compounds with smaller surface areas. Temperature also plays a role in sulfur oxidation. Under field conditions, sulfur oxidation generally increases with higher temperatures. This means that oxidation is typically more pronounced during the summer than in winter, assuming other factors remain constant. The optimal temperature range for sulfur oxidation is between 27 to 35°C. However, in forested ecosystems, these temperatures may not be reached at the litter surface. Extreme temperatures above 55 to 60°C can be detrimental to soil microorganisms, but such conditions are unlikely to occur in forest soils.

Soil texture and moisture content are interconnected factors that affect sulfur oxidation. Texture influences aeration, which in turn affects moisture levels. Therefore, the effects of moisture and texture on sulfur oxidation cannot be separated, and both factors are believed to influence oxidation rates. The highest oxidation rates are observed near field capacity, which is the moisture level at which the soil retains the maximum amount of water. Adequate oxygen availability is necessary for oxidation by aerobic microorganisms, and moisture is essential for microbial activity. However, different soil textures retain varying amounts of moisture at field capacity, leading to different rates of sulfur oxidation (Tisdale and Nelson, 1975).

1.7. The oxidation of sulfur is a crucial stage in the sulfur cycle due to several reasons

A. In many soils, sulfur is present in reclaimed forms, such as S minerals and certain fertilizers and modifiers.

However, plants and most microorganisms can primarily absorb sulfur in the oxidized form as sulfate. Therefore, sulfur oxidation is essential to convert the reclaimed forms into the absorbable sulfate form (Janzen and Bettany, 1987).

B. Applying sulfur to the soil serves multiple purposes, including supplying sulfur to plants, modifying the soil, and improving plant nutrition by releasing other nutrients like phosphorus, iron, zinc, and manganese. These benefits are achieved when sulfur is adequately oxidized in the soil (Janzen and Bettany, 1987).

C. The oxidation of sulfur compounds in the soil serves as an energy source for a group of microorganisms known as sulfur oxidizers, particularly bacteria of the *Thiobacillus* genus. These microorganisms play a beneficial role in land improvement and plant nutrition. Their importance should not be overlooked (Janzen and Bettany, 1987).

D. Increasing the solubility of nutrients in calcareous soils is a significant challenge in crop production. Calcareous soils, characterized by high pH and calcium ion concentrations, often fix phosphorus and certain micronutrients, making them unavailable to plants. This nutrient-fixing mechanism reduces crop yields. Researchers have explored methods to overcome this issue by acidifying the soil and lowering the pH. Sulfur and sulfuric acid have been commonly used for this purpose, leading to positive outcomes in terms of reducing nutrient stabilization and increasing nutrient solubility in these soils (Deluca et al., 1989; Pathiratn et al., 1989; Rosa et al., 1989; Tisdale et al., 1984).

Sulfur oxidation is crucial for making sulfur accessible to plants and microorganisms, increasing soil fertility, and enhancing the solubility of nutrients in various soil types.

1.8. Sulfur-Oxidizing Bacteria: Key Players in Sulfur Cycling

The diversity and abundance of sulfur-oxidizing bacteria have been studied in various terrestrial environments, sulfide-removing bioreactors, and coastal aquaculture settings. These investigations have involved analyzing functional genes (Tourna et al., 2014; Varon-Lopez et al., 2014; Xia et al., 2014; Lou et al., 2011; Krishna et al., 2010).

Sulfur oxidation in soil is primarily carried out by microorganisms, including fungi and bacteria. The ability of fungi to oxidize sulfur was discovered almost a century ago (Abbott, 1923). However, bacteria are generally considered to be more efficient than fungi at oxidizing elemental sulfur (ES), especially in silty soils (Czaban and Kobus, 2000). Sulfur-oxidizing bacteria in soil are mainly chemolithotrophs, which obtain electrons from reduced sulfur compounds for respiration and assimilate carbon dioxide (Friedrich et al., 2005; Tourna et al., 2014). These chemolithotrophs exhibit biochemical and physiological diversity, as evidenced by their ability to utilize different substrates and variations in energy conservation from the same substrates among different species (Gosh and Dam, 2009). The microorganisms that play a role in sulfur oxidation are tolerant of acidic soils and low pH levels. Significant oxidation can occur in acidic soils, with maximum rates often observed at pH levels below 4 (Barton, 1978). *Thiobacillus* bacteria have been reported to perform oxidation even at pH 9 (Brady, 1984), indicating that soil pH alone does not typically limit sulfur oxidation significantly (Kennedy, 1986).

The biological oxidation of sulfur in soil is performed by various microorganisms, including fungi, bacteria, and actinomycetes. These microorganisms can be classified into three main groups: heterotrophic microorganisms, photo lithotrophic bacteria, and chemo lithotrophic bacteria.

a) Heterotrophic microorganisms: This group primarily utilizes organic compounds as a source of carbon and energy. In aerobic conditions, they use oxygen and sulfate as electron acceptors for the oxidation process.

b) Photo lithotrophic bacteria: These bacteria possess a specific type of chlorophyll known as bacteriochlorophyll and carry out non-oxygenic photosynthesis. They are mainly active in anaerobic conditions and are typically found in aquatic environments. In agricultural soils, they are not as significant as other sulfur oxidizers.

c) Chemolithotrophs: This group of bacteria can be further divided into three categories: obligate, facultative, and mixotrophic. These bacteria utilize various forms of reclaimed sulfur compounds such as hydrogen sulfide, metal sulfides, polysulfides, and elemental sulfur as an energy source. Through the oxidation of these compounds, they derive energy. Microorganisms in this group have the ability to convert sulfide ions into elemental sulfur or sulfate. The energy released during these reactions is substantial.

$$H_2S + 1/2\ O_2 \rightarrow H_2O + S \qquad \Delta G^0 = -\ 52.1\ \text{Kcal/mol}$$

$$S + 3/2\ O_2 + H_2O \rightarrow H_2SO_4 \qquad \Delta G^0 = -\ 145.5\ \text{KCal / mol}$$

Thiobacillus bacteria, along with certain heterotrophic bacteria, photosynthetic sulfur bacteria, and colorless sulfur bacteria, are capable of sulfur oxidation in soil. However, among these species, *Thiobacillus* and heterotrophs play a particularly important role in soil sulfur oxidation (Tate, 1995).

Bacteria belonging to the genus *Thiobacillus* are considered the most significant sulfur-oxidizing microorganisms in soil. These bacteria can have a population density of more than one million per gram of soil (Rupela and Taura, 1973). *Thiobacillus* are gram-negative, rod-shaped bacteria, typically ranging in length from 1 to 4 μm. They are chemolithotrophs, meaning they obtain energy from reclaimed sulfur compounds, and some species are motile, possessing either a flagellum or polar flagella. Importantly, none of the *Thiobacillus* species are known to be pathogens. *Thiobacillus* are capable of utilizing carbon dioxide for assimilation and are classified into different types based on their nutritional requirements. Some species are obligate chemolithotrophs, meaning they strictly rely on inorganic compounds as energy sources, while others are selective chemolithotrophs or mixotrophs. Most Thiobacillus species are aerobic, but there is one species, *Thiobacillus denitrifican*s, that can perform denitrification under anaerobic conditions by utilizing nitrate as a terminal electron acceptor. Within the genus *Thiobacillus*, twenty-one species have been identified. These species can be further categorized into two groups based on their optimal pH range for activity: neutral (with an optimum pH around 7) and acidophilic (with an optimum pH around 3). *Thiobacillus* species are commonly found in various environments such as soil, sulfur deposits, acid effluents, wastewaters, lakes, and both saline and freshwater swamps. The first identified species of the Thiobacillus genus is *Thiobacillus thioparus* (formerly known as *Thiobacillus thiooxidans*), which was described by Gerinck in 1904. It serves as a typical representative of the *Thiobacillus* genus (Kelly and Harrison, 1989).

Thiobacillus bacteria have the ability to oxidize various sulfur compounds, including elemental sulfur, and derive the energy required for their growth, activity, and proliferation. However, the population of sulfur-oxidizing microorganisms, including *Thiobacillus*, is not significant in arid soils that lack organic matter and moisture content. In such conditions, the distribution of these microorganisms in the soil is limited. Nevertheless, even in arid soils, a small number of bacteria can still be present, typically ranging from 100 to 200 cells per gram of soil. The population of sulfur-oxidizing bacteria in these soils can increase when sulfur-amended materials are added, leading to an intensification of sulfur oxidation in subsequent seasons (Tabatabai, 1986). The presence of *Thiobacillus* bacteria in natural environments is dependent on the availability of sulfur compounds that can be utilized as an energy source. Since *Thiobacillus* bacteria are chemolithotrophs, their survival and activity are closely linked to the presence of suitable sulfur compounds for oxidation (Kelly and Harrison, 1989).

1.9. Importance of SOB in sulfur mineralization and availability to plants

Thiobacillus bacteria, being the primary sulfur oxidizers in agricultural soils, play a crucial role in the production of sulfuric acid through the oxidation of sulfur. This process can lead to a significant decrease in soil pH, particularly in environments with low buffering capacity. When *Thiobacillus* is inoculated with sulfur, the oxidation of sulfur is enhanced, resulting in a greater effect on pH reduction. In fact, at various sulfur levels, the inoculation of *Thiobacillus* tends to cause a higher reduction in pH compared to non-bacterial treatments. The production of sulfuric acid by *Thiobacillus* bacteria occurs concurrently with sulfur oxidation. If the soil has low buffering capacity, this acid production can further contribute to a decrease in pH (Vishniac and Santer, 1957). In many regions around the world, such as New Zealand, Sri Lanka, and Australia, sulfur is mixed with phosphorus fertilizers to enhance their efficiency. Since sulfur oxidation in soil is generally slow, sulfur-oxidizing microorganisms, especially *Thiobacillus*, are employed to intensify the process. For instance, in Sri Lanka, where there are abundant apatite mines, a mixture of apatite, sulfur, and *Thiobacillus* bacteria is used to produce a phosphorus fertilizer known as "bio superphosphate" (Pathiratna et al., 1989). This approach helps to improve the availability and accessibility of phosphorus for plant uptake.

In a study that was conducted, the researchers investigated the factors that affect sulfur oxidation in soils treated with elemental sulfur and phosphate rocks. They divided the soils into two groups: one group was inoculated with *Thiobacillus* bacteria, while the other group served as a control without any inoculation. They used a soil suspension enriched with sulfur and *Thiobacillus* bacteria as the inoculant. The results of the study showed that after two weeks of incubation, the amount of sulfur oxidized in the inoculated soils was 11 times higher compared to the non-inoculated soils. After four weeks, the sulfur oxidation rate was 23% in the non-inoculated soils and 54% in the inoculated soils. This indicates that the presence of *Thiobacillus* bacteria significantly increased the sulfur oxidation in the soil. The study also found that the number and types of *Thiobacillus* bacteria present in the soils played a role in determining the amount of sulfur oxidation. Different species or strains of *Thiobacillus* bacteria may have different capabilities in oxidizing sulfur.

Furthermore, the study examined the relationship between the ratio of phosphate to sulfur rock and the yield and phosphorus uptake by rye plants. It was observed that the yield and phosphorus uptake were influenced by this ratio. The amount of phosphorus released from the phosphate rock depends on the extent of sulfur oxidation and the production of sulfuric acid. As a result, there was an inverse relationship between the phosphate to sulfur ratio and the yield and phosphorus uptake by rye plants. Overall, this study provides insights into the role of *Thiobacillus* bacteria in promoting sulfur oxidation in soil and its implications for phosphorus availability and plant growth. (Attoe and Olson, 1966).

Deluca et al. (1989) conducted a study to investigate the impact of sulfur and *Thiobacillus* inoculation on phosphorus availability in three calcareous soils, both in a greenhouse and on a farm. They applied various treatments, including inoculation with *Thiobacillus thiopareus*, sulfur alone, sulfur and inoculation, triple superphosphate (TSP) alone, TSP and sulfur, and TSP and inoculation. After 8 weeks, wheat was harvested, and measurements were taken for yield, phosphorus uptake by wheat, and soil pH. The results of the study revealed that sulfur consumption combined with *Thiobacillus* inoculation significantly reduced soil pH compared to non-inoculated sulfur treatments. Furthermore, sulfur supplementation with TSP in both inoculated and non-inoculated treatments led to a significant decrease in soil pH compared to sulfur alone and superphosphate treatments. The increased phosphorus consumption likely stimulated the activity of *Thiobacillus* bacteria. Across all three soil types, the sulfur and superphosphate treatments exhibited significantly higher phosphorus uptake and available P compared to the superphosphate (TSP) treatment. In another experiment conducted in Arkansas, the effects of potassium sulfate and elemental sulfur fertilizers on wheat were investigated. The results indicated a 90% increase in wheat yield with elemental sulfur fertilizers and a 190% increase with potassium sulfate. However, sulfur had a lower yield compared to potassium sulfate, likely due to slower oxidation rates. Since sulfur oxidation is primarily a biological process in soils, environmental factors that influence the population and activity of sulfur-oxidizing microorganisms, such as *Thiobacillus*, can impact sulfur oxidation. The rate of biological sulfur oxidation in soils depends on the population of *Thiobacillus* bacteria, the size of elemental sulfur particles, and environmental conditions. These bacteria also require essential nutrients, which is why sulfur oxidation tends to be faster in fertile soils (Agrifacts, 2003).

The application of *Thiobacillus* inoculation has been shown to increase sulfur oxidation (Besharati, 1998). Several studies have reported that soil inoculation with *Thiobacillus* spp. can enhance sulfur oxidation by a factor of 1 to 11 (Kittams and Attoe, 1965). However, when the bacteria were inoculated without sulfur application, only trace amounts of sulfur compounds were recovered, which is likely a result of the natural sulfur cycle in the soil (Bardiya et al., 1982; Killham, 1994; Tabatabai, 1986). Many researchers have reported the positive effect of soil inoculation with *Thiobacillus* bacteria on increasing phosphorus uptake (Attoe and Olson, 1966; Pathiratna et al., 1989; Khavazi et al., 2001; Kittams and Attoe, 1965; Rosa et al., 1989; Deluca et al., 1989; Besharati, 2000). *Thiobacillus* bacteria, being the primary sulfur oxidizers in agricultural soils, obtain energy for CO2 stabilization and perform vital activities through the oxidation of sulfur-reclaimed compounds (Kelly and Harrison, 1984). The sulfur oxidation by sulfur-oxidizing bacteria and the subsequent local reduction in soil pH around plant roots increase the solubility of stabilized elements in calcareous soils (Cifuentes and Lindemann, 1993), ultimately leading to increased uptake of these elements by plants (Besharati, 1998; Rosa et al., 1989).

Indeed, several researchers have reported the beneficial effects of sulfur application in calcareous soils and soils with high pH on nutrient uptake, including phosphorus, zinc, and iron. Studies conducted by Besharati (2000), Deluca (1989), Kalbasi et al. (1988), Kaplan and Orman (1998), Khan et al. (1986), Kittams and Attoe (1965), Modaihsh et al. (1989), and Pathiratna et al. (1989) have all documented these positive effects. Sulfur application has been shown to enhance the availability and uptake of these essential nutrients by plants in such soil types.

1.10. Sulfur Applications for Soil and Plant Nutrition Improvement

To address iron deficiency in calcareous soils and enhance the relative solubility of iron in the soil, researchers such as Tisdale et al. (1993), Modaihsh et al. (1989), and Kaplan and Orman (1998) have suggested the addition of sulfur. It is known that calcareous and alkaline soils pose challenges for the absorption of elements like iron, zinc, and phosphorus (Tisdale et al., 1993; Modaihsh et al., 1986; Kaplan and Orman, 1998). The use of sulfur has been a long-standing approach to tackle this problem (Tauro and Rupela, 1973; Tisdale et al., 1993; Razeto, 1982; Kalbasi et al., 1988).

The application of sulfur in agricultural lands aims to supply the necessary sulfate for plant growth (Singh et al., 1991; Singh and Chhibba, 1991; Singh and Chaudhari, 1997). Additionally, it contributes to the improvement of alkaline and saline soils (Rupela and Taura, 1973; Venkatakrishanan and Abrol, 1981), increases the solubility of certain nutrients, and ultimately enhances plant nutrition in calcareous soils (Kaplan and Orman, 1998; Razeto, 1982; Kalbasi et al., 1998). Furthermore, the addition of organic matter to the soil has also been suggested as a means to address iron deficiency and modify the pH of calcareous soils (Malakooti & Homaei, 2003).

Elemental sulfur, by itself, is inert, and its beneficial effects depend on oxidation and conversion to sulfate (Tabatabai, 1986). Since sulfur oxidation in soil is predominantly a biological process, various environmental conditions and parameters such as pH, moisture, ventilation, temperature, soil fertility, and the population of sulfur-oxidizing microorganisms affect the rate and intensity of sulfur oxidation (Attoe and Olson, 1966; Stevenson and Cole, 1999; Tisdale et al., 1993; Chapman, 1989; Nor and Tabatabai, 1977).

Kalbasi et al. (1988) conducted a field experiment to examine the impact of sulfur on the uptake of iron (Fe), zinc (Zn), and manganese (Mn) by corn, sorghum, and soybean plants in a clay loam soil with 40% lime. Powdered sulfur at rates of 0, 100, 200, and 400 kg/ha was added to the soil before planting. The results demonstrated that sulfur application significantly reduced soil pH and bicarbonate concentration, while increasing the availability of DTPA-extractable Fe, Mn, and Zn in the soil. Moreover, the treatments exhibited a significant increase in yield, iron and zinc content in the plants compared to the control. Notably, iron deficiency-induced chlorosis was eliminated in all treatments except the control. These findings indicate that sulfur application is effective in mitigating iron chlorosis and enhancing yield in calcareous soils.

In a greenhouse experiment conducted by Miller (1965), the effects of calcium sulfate and elemental sulfur on the utilization of rock phosphate phosphorus were compared. The study found that calcium sulfate had no significant impact on clover growth. However, the application of sulfur at rates ranging from 600 to 800 kg/ha significantly increased clover yield and the absorption of phosphorus.

The effect of elemental sulfur (ES) application on alkaline soils and its impact on soil pH and phosphorus uptake were investigated at Iran's Ministry of Petroleum Research Center. The results showed that the addition of 2 tons/ha of elemental sulfur decreased soil pH and simultaneously increased the availability of phosphorus in the soil, without requiring significant amounts of phosphorus fertilizers, based on the plant's needs (Besharati, 1998).

Madiyesh et al. (1989) conducted greenhouse experiments to examine the effect of elemental sulfur on the chemical properties and nutrient availability in calcareous soils. Three different calcareous soils with varying textures, lime content, phosphorus levels, and micronutrients were treated with elemental sulfur at concentrations of 0.5%, 1.5%, and 3% (w/w%). The soil columns were incubated at 30°C, and soil samples were collected after 3, 6, 9, and 18 weeks to analyze the nutrient and chemical properties of the soil. The results indicated that the consumption of 0.5% elemental sulfur in all three soil types significantly decreased soil pH compared to the control. Additionally, soluble sulfate, electrical conductivity (EC), iron (Fe), manganese (Mn), copper (Cu), and available phosphorus all significantly increased compared to the control, while available zinc (Zn) content showed no significant change. The researchers suggested that the extent of nutrient availability changes depended on the lime content and the lime-to-clay ratio in the soil. In soils with lower lime content and lime-to-clay ratio, the impact of sulfur consumption was more pronounced. In soils with higher buffering properties, significant increases in Fe and Cu were observed only at high levels of sulfur application.

Jaggi et al. (2005) conducted a study to assess the impact of elemental sulfur (ES) application under different moisture and temperature regimes on pH and phosphorus availability in three soil types: acidic (pH=4.9), neutral (pH=7.1), and alkaline (pH=10.2). The results indicated that sulfur oxidation led to a decrease in pH in alkaline soils, consequently increasing the concentration of available phosphorus. The process of sulfur oxidation was influenced by soil temperature and moisture, and it had the potential to enhance soil pH and increase the availability of phosphorus. The highest reduction in pH in alkaline soil, without sulfur application, was observed under waterlogged conditions. In calcareous soil with sulfur application, the most significant reduction in pH occurred under 60% moisture conditions, which coincided with rapid sulfur oxidation. This improved soil conditions for better access to essential elements.

Kuchar et al. (1990) conducted an experiment where they added elemental sulfur (ES) at different rates (0, 30, 60, and 120 mg) to soil with a pH of 7.8 and an absorbable sulfate content of 4.5 mg/kg. The study focused on corn yield, and the results showed that the control without sulfur had a yield of 6.4 g/pot. However, with sulfur application, the average yield increased to 13.6 g/pot. The highest corn yield (14.95 g/pot) was achieved with 30 mg of sulfur per pot, and further increases in sulfur application did not have a significant effect on yield. Sulfate uptake by corn plants increased significantly with higher sulfur content, with sulfate absorption amounts of 2.5, 12.4, 13.3, and 18.1 mg/pot for the 0, 30, 60, and 120 mg sulfur treatments, respectively.

Dubai and Beyer (1995) investigated the effects of elemental sulfur (ES) application on soybean yield, nitrogen fixation, and the number of nodes in a calcareous soil. Different rates of sulfur (0, 10, 20, 30, and 40 kg per hectare) were applied. The study found no significant difference in the dry weight of soybean plants between the 0 and 10 kg/ha sulfur treatments. However, treatments with 20, 30, and 40 kg/ha sulfur resulted in increased plant dry weight by 17.44%, 29.65%, 29.9%, and 32.32%, respectively.

Scherer and Lank (1996) conducted a pot study to evaluate the effects of different sulfur levels (0, 2.5, and 20 mg sulfur per kg of soil) on the yield, nitrogen uptake, and acetylene reduction of leguminous plants such as mungbean, clover, alfalfa, and chickpea. The results showed that the highest shoot dry weight of plants was obtained with the application of 20 mg sulfur per kg of soil. The number of nitrogen nodules and the rate of acetylene reduction exhibited a positive and significant correlation with increasing sulfur levels in the plants.

2. Conclusion, Recap of key findings on sulfur and SOB dynamics

Implications for improving soil health and agricultural sustainability

In conclusion, the studies reviewed provide compelling evidence for the positive impact of SOB on soil properties and soil management. Sulfur application, particularly in conjunction with SOB, has demonstrated its potential in addressing soil alkalinity, salinity, and acidity, leading to improved soil conditions and enhanced crop productivity. The research findings highlight the importance of considering regional variations in soil characteristics and microbial dynamics when implementing sulfur-based interventions. Positive outcomes have been observed in specific regions such as Golestan and Azerbaijan (Urmia) provinces in Iran, while the effects may be limited or vary in other areas. Hence, it is crucial to tailor sulfur application strategies based on local soil conditions and microbial interactions. The interactions between sulfur and SOB play a critical role in sulfur transformation processes, enhancing the efficacy of sulfur application. The presence of sulfur-oxidizing bacteria, such as *Thiobacillus*, facilitates sulfur oxidation, leading to reduced soil pH and improved nutrient availability. These microbial activities contribute to the overall health and fertility of the soil. Furthermore, sulfur application has shown promise in improving soil physical properties, including water infiltration, soil structure, and nutrient uptake by plants. By reducing soil alkalinity and increasing nutrient availability, sulfur application offers opportunities for sustainable soil management and enhanced agricultural productivity. However, it is important to consider site-specific factors, such as soil type, climate, and cropping systems, when implementing sulfur-based interventions. Optimal sulfur application rates and timing should be determined to maximize its benefits without causing any adverse effects on soil health.

The implications of sulfur application and the role of sulfur-oxidizing bacteria (SOB) in improving soil health and agricultural sustainability are significant. Here are some key implications:

Soil Fertility Enhancement: Sulfur application, coupled with SOB activity, improves soil fertility by increasing the availability of essential nutrient elements. The presence of sulfate ions resulting from sulfur oxidation promotes optimal plant growth and development. This can lead to increased crop yields and improved agricultural productivity.

Soil pH Regulation: Sulfur oxidation by SOB contributes to the regulation of soil pH. The conversion of elemental sulfur into sulfate ions creates an acidic environment, which can help to neutralize alkaline soils. This is particularly beneficial in regions with high soil pH or alkalinity, where nutrient availability is often limited. The adjustment of soil pH through sulfur application can enhance nutrient uptake by plants and improve overall soil health.

Nutrient Management: The interaction between sulfur and SOB has implications for nutrient management in agriculture. Sulfur application can improve the solubility and availability of certain essential nutrients, such as phosphorus, iron, and zinc, especially in alkaline or calcareous soils. This reduces the need for excessive fertilizer application, leading to more efficient nutrient use and minimizing the risk of nutrient runoff and environmental pollution.

Soil Organic Matter Decomposition: SOB activity contributes to the decomposition of organic matter in the soil. This promotes nutrient mineralization and release from organic compounds, making them accessible to plants. Improved organic matter decomposition enhances nutrient cycling and availability, which is crucial for maintaining soil fertility and sustaining agricultural productivity.

Soil Structure and Water Management: The activity of SOB can improve soil structure by promoting soil particle aggregation. Enhanced soil aggregation improves water infiltration, reduces soil erosion, and increases water-holding capacity. This leads to better water management, increased soil resilience to drought, and improved plant water uptake efficiency.

Sustainable Agriculture Practices: The integration of sulfur application and management of SOB into agricultural practices can contribute to sustainable agriculture. By optimizing nutrient availability, reducing fertilizer requirements, and improving soil health, these practices support environmentally friendly and economically viable farming systems. They help minimize the negative impacts of agriculture on soil degradation, water quality, and ecosystem health.

In conclusion, sulfur application and the role of sulfur-oxidizing bacteria have wide-ranging implications for improving soil health and agricultural sustainability. These practices enhance nutrient availability, regulate soil pH, promote organic matter decomposition, improve soil structure, and support sustainable nutrient management and water use. By implementing these strategies, farmers can enhance soil fertility, increase crop productivity, and contribute to the long-term sustainability of agricultural systems.

2.1. Future prospects for advancing knowledge in this field

The field of sulfur application and SOB in soil management holds promising avenues for future research and knowledge advancement. Here are some potential areas of focus:

Mechanistic understanding: Further research is essential to enhance our understanding of the mechanisms involved in sulfur oxidation and its interaction with sulfur-oxidizing bacteria (SOB). By investigating the genetic and metabolic pathways associated with sulfur oxidation, we can gain valuable insights into the enzymatic processes and microbial interactions that drive these transformations. Clarifying the specific roles of various sulfur-oxidizing bacterial species and their interactions with other soil microorganisms will contribute to a more comprehensive understanding of sulfur cycling in soils.

Microbial ecology: Investigating the microbial ecology of SOB and their interactions with soil microbial communities (Basharti H (2006) is essential. Examining the factors that influence the abundance, diversity, and activity of SOB in different soil types and environmental conditions can help identify key drivers and their effects on sulfur transformation processes. This understanding can inform the development of targeted interventions to enhance SOB populations and optimize sulfur oxidation in soils.

Soil specific approaches: Researching the effects of sulfur application and SOB management in a wider range of soil types and geographical regions is crucial. Soil characteristics, such as texture, pH, organic matter content, and microbial composition, can influence the effectiveness of sulfur-based interventions. Understanding the soil-specific responses to sulfur application can enable the development of tailored strategies for different agricultural systems and geographic locations.

Agronomic practices: Investigating the integration of sulfur application and SOB management with other agronomic practices is an important area of exploration. Assessing the combined effects of sulfur application with different nutrient management strategies, crop rotations, and tillage practices can provide insights into synergistic interactions and potential trade-offs. This can help optimize the integration of sulfur-based interventions into sustainable agricultural systems.

Climate change implications: Assessing the impacts of climate change on sulfur cycling and the role of SOB in soil management is crucial. Climate change can influence soil microbial communities, soil processes, and nutrient dynamics. Understanding how changing climatic conditions affect sulfur oxidation, microbial activity, and the availability of nutrients in soils will be essential for adapting soil management strategies to future climates.

Technological advances: Advancements in molecular techniques, such as metagenomics, metatranscriptomics, and stable isotope probing, can provide powerful tools for studying sulfur-oxidizing bacteria and their functions in soil ecosystems. Integrating these techniques with high-throughput sequencing and omics approaches can offer a more comprehensive understanding of microbial community dynamics, gene expression, and metabolic pathways involved in sulfur oxidation.

In conclusion, future research in the field of sulfur application and sulfur-oxidizing bacteria should focus on deepening our mechanistic understanding, exploring microbial ecology, tailoring approaches to specific soils, integrating sulfur management with agronomic practices, considering climate change implications, and leveraging technological advancements. Advancing knowledge in these areas will contribute to more effective and sustainable soil management strategies, enhancing agricultural productivity and environmental sustainability.

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