



Biodegradation and bioavailability of low-molecular-weight dissolved organic sulphur in soil and its role in plant-microbial S cycling

Qingxu Ma · Congyue Tou · Sheng Tang ·
Deying Wang · Wankun Pan · Lianghuan Wu ·
Davey L. Jones

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Abstract

Background Plant sulphur (S) deficiency occurs worldwide; however, in comparison to other macronutrients (e.g., N, P), limited attention has been paid to the content, composition, bioavailability, and cycling of S in soil. An increased knowledge of S biogeochemical cycling, however, can aid soil S management and plant S nutrition.

Scope This review discusses current knowledge on the bioavailability and decomposition of soil-soluble organic S, focusing mainly on proteins and two S-containing amino acids (methionine (Met) and cysteine (Cys)).

Conclusions Proteins represent the major S input into soil with most held within insoluble organic matter and a lesser proportion present as dissolved organic S (DOS). The size of the DOS pool

is typically much lower than that of the inorganic SO_4^{2-} pool, however, this reflects the rapid turnover and replenishment of this pool, which is orders of magnitude faster than the inorganic S pool, reflecting the importance of soil organic S cycling. Soluble proteins can be decomposed to SO_4^{2-} within minutes, and S-containing amino acids can be mineralised within seconds to hours. Microorganisms utilise S-containing amino acids in three steps: uptake into the microbial biomass within seconds; release of CO_2 , NH_4^+ , and SO_4^{2-} within minutes to hours; and the re-utilisation of released inorganic S and nitrogen (N) by microorganisms and plants. Current evidence suggests that Met and Cys play limited roles in plant N nutrition due to intense competition from soil microbes and the supply of inorganic N in fertilisers, however, these amino acids can account for ca. 10% of total plant S uptake (intact form and the inorganic

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Q. Ma · C. Tou · S. Tang · W. Pan · L. Wu
Ministry of Education Key Lab of Environmental
Remediation and Ecosystem Health, College
of Environmental and Resource Sciences, Zhejiang
University, Hangzhou 310058, China

Q. Ma (✉) · S. Tang · D. Wang · D. L. Jones
School of Natural Sciences, Bangor University,
Gwynedd LL57 2UW, UK
e-mail: afpade@bangor.ac.uk

D. Wang
School of Life Sciences, University of Warwick,
Coventry CV4 7AL, UK

L. Wu
Zhejiang Provincial Key Laboratory of Agricultural
Resources and Environment, College of Environmental
and Resource Sciences, Zhejiang University,
Hangzhou 310058, China

D. L. Jones
SoilsWest, Centre for Sustainable Farming Systems,
Food Futures Institute, Murdoch University, Murdoch,
WA 6150, Australia

S derived from them). We conclude that direct uptake of S-containing amino acids by microbes, and to a lesser extent plants, is an effective and energy efficient way to bypass the SO_4^{2-} pool and that the production and consumption of DOS cycling represents the key central cog in soil S cycling.

Keywords Sulphur deficiency · Plant sulphur uptake · Sulfate · Soil-soluble organic sulphur · Sulphur bioavailability · S-containing amino acids · Sulphur turnover

Introduction

Sulphur (S) is a macronutrient essential for plant growth and development, typically constituting 0.3–0.5% of the total dry plant weight (Grant et al. 2012; Kovar 2021). In agricultural systems, oil-seed crops and cruciferous vegetables have a high S demand, requiring 30–40 kg S ha⁻¹ y⁻¹, whereas cereals only require 15–20 kg S ha⁻¹ y⁻¹ for optimum growth (Scherer 2001). S plays a crucial role in many plant metabolic processes, including the synthesis of amino acids (e.g., methionine (Met) and cysteine (Cys), biotin, coenzyme A, glutathione, thiamine, chlorophyll, membrane sulfolipids and cell wall components (Narayan et al. 2022). Furthermore, S acts in the synthesis of secondary S compounds, such as glucosinolates and alliin, as well as N₂ fixation by leguminous plants (Piotrowska-Długosz et al. 2017). In addition, as the bioavailability and mobility of heavy metals are closely linked to the biogeochemical cycling of S in soil, S amendments can decrease heavy metal accumulation in plants and also aid in detoxification via the production of S-containing phytochelatins (Cobbett 2000; Liu et al. 2021; Zakari et al. 2021).

Although S is crucial for plant growth, in comparison to nitrogen (N) and phosphorus (P) it has received relatively little attention because atmospheric S deposition and fertiliser inputs normally supply enough S to satisfy plant demand (Borja Reis et al. 2021). However, S deficiency has become an increasing problem worldwide over the last 25 years (Feinberg et al. 2021), mainly due to (i) the use of low S or even S-free fertilisers, such as triple superphosphate, which contains low amount of S (Chalk et al. 2017); (ii) reductions in gaseous air pollution (i.e. SO₂) resulting from strict emission regulations

(Oulehle et al. 2011); (iii) the introduction of higher yielding crop cultivars; (iv) reduced S return of farmyard manure and organic wastes; (v) soil degradation and loss of organic matter; (vi) poor availability of S fertilisers; and (vii) insufficient testing of soil S status by farmers (Divito et al. 2015; Grant et al. 2012; Piotrowska-Długosz et al. 2017; Rhymes et al. 2021). With marked decrease in S deposition across Europe and North America, S is now a limiting nutrient for agricultural production (Zhao et al. 2002). In Asia, approximately 39% of Indian soil was classed as deficient in S (Joshi et al. 2021), and an investigation from 1997 to 2003 showed that approximately 30% of agricultural soils in China were S-deficient (Fan 2005). Thus, the increasing recognition of soil S deficiency is concerning and requires urgent attention if we are to meet global food security targets (Joshi et al. 2021; Michalovicz et al. 2021).

Due to its key role in photosynthesis and protein production, the shortage of S has been shown to greatly reduce the yield of many crops, reducing their quality and subsequent marketability and usability (Małgorzata et al. 2016). For example, oilseed rape is particularly sensitive to S limitation, and S deficiency reduced its growth and yield greatly (Scherer 2001). S deficiencies severely impair grain fill and kernel quality in maize greatly reducing yields (Aula et al. 2019; Carciochi et al. 2019a; Pias et al. 2019) and has become a yield-limiting factor in many countries (Carciochi et al. 2018). S deficiencies also reduce the quality of baked wheat products because the S-containing amino acids in the gluten fraction of flour are responsible for the elasticity of the dough and bread volume (Piotrowska-Długosz et al. 2017). Dual S and N deficiency compromises crop yields in some cropping systems (Carciochi et al. 2020; Tavakoli Kivi and Bailey 2017); this is particularly a serious problem in organic farming systems, because mineral fertilisers and other chemical compounds are often prohibited. In addition, S and N are metabolically linked, and the lack of adequate S to convert N into plant biomass may increase N losses from agricultural soils (i.e. NO₃⁻ leaching, N₂O and NH₃ emissions; Blum et al. 2013; Bon and Monteiro 2010). Furthermore, crops grown in soil with insufficient levels of S will provide insufficient levels of S-containing amino acids in animal feed and foods destined for human consumption. It should be noted, however, that S deficiency in humans is relatively rare unless insufficient protein is

consumed (Komarnisky et al. 2003). To promote sustainable S cycling in agroecosystems, more intensive studies on soil S content, variability, cycling dynamics, and plant bioavailability are necessary. This is not limited to the organic farming systems, although S deficiency can be alleviated by applying mineral S in both organic and conventional farming. However, in such cases, for this fertilisation to be efficient, farmers must be aware of when and how much fertiliser to apply (Boye et al. 2009).

Therefore, the focus of this review will be to critically evaluate the existing literature on the bioavailability and decomposition of soil-soluble organic S, mainly focusing on proteins and two S-containing amino acids: Cys and Met. We focus on these compounds as protein is the dominant form of organic-S entering soils due to root and microbial turnover and the addition of other organic wastes (e.g., crop residues, manures, biosolids etc.). When SO_4^{2-} is in short supply in soil, native soil-soluble organic S also provides the vital link in the S cycle as its microbial turnover leads to the production of inorganic S. The review will also focus mainly on S cycling in agroecosystems, however, for comprehensive reviews on S cycling in wetlands see Wu et al. (2013) and Karimian et al. (2018).

Forms of S in soil

S is present in soils as both organically bonded S and inorganic S. Organic S generally accounts for 90–95% of the total S in well-aerated soils, while inorganic S only accounts for less than 5% of the total S pool in humid tropical and temperate soils (Boye et al. 2010; Dawit et al. 2009; Eriksen 2009; Kopittke et al. 2016; Scherer 2009). In general, inorganic S species can be operationally fractionated into water-soluble sulphate, adsorbed sulphate, dilute-HCl soluble S, volatile S, and pyritic S (Johnson et al. 1981; Scherer 2009). Typically, most is present as water soluble S in most agricultural soils above pH 6 (Schmalz et al. 2001). In the case of soil organic S, it is usually classified into three main groups: (i) C-bonded S (chemical group C–S, mainly amino acids), (ii) ester-bonded S (chemical groups C–N–S, C–O–S, and C–S–S), and (iii) residual S. Organic S is generally detected as a heterogeneous mixture (total amount) and lacks the identity of specific S-containing molecules limiting our ability to assess its functional significance (Bon and Monteiro, 2010; Kertesz 2004). Continued advances in S-based

metabolomics, alongside the more general application of metabolomics in soil, however, opens the possibility to improve our understanding of the individual metabolites comprising the different organic S pools in soil (Kasamatsu et al. 2021; Kellogg and Kang 2020; Pohlabeln and Dittmar 2015; Withers et al. 2020). Although plants mainly absorb S as sulphate, organic S compounds especially those which are soluble and of low molecular weight (< 1000 MW) may represent important S sources for plants (Bon and Monteiro, 2010; Goh and Pamidi 2003). Our poor understanding of the different organic S compounds in solution and their relative concentration, however, is limiting our capacity to predict the importance of organic S uptake by plants and microorganisms.

C-bonded S includes S-containing amino acids (i.e. homocysteine, taurine, Cys and Met, of which only Cys and Met are biosynthetically incorporated into proteins), as well as mercaptans and disulphides (Scherer 2001). C-bonded S is the most labile fraction of soil organic S, existing primarily as proteins in agricultural soils, and is estimated to comprise 20–40% of soil S (King and Klug 1982); this correlates with the size of the microbial biomass and represents a structural form, rather than a storage form, in the microbial biomass. Ester-bonded S (oxidised fractions) typically comprises 35–60% of the organic S pool, with contents more commonly at the lower end of this range (Fakhraee et al. 2017). For example, in forest soils, the total S pool is 820–1,270 mg kg^{-1} (dry weight), mostly present as organic S (ester sulphate S: 301–769 mg kg^{-1} ; C-bonded S: 426–505 mg kg^{-1}). Phosphate-extractable sulphate S accounts for only 17–79 mg kg^{-1} (Tanikawa et al. 2014). Soil microbial biomass S generally accounts for 1.5–5.0% of the total organic S but is probably one of the most dynamic S pools in soil (Scherer 2001). Other minor fractions include coenzymes, sulpholipids, contributing minimally to the total soil S content (King and Klug 1982). Although the evidence base is weak, more ester bonded S was found in non-rhizosphere (bulk) soil than in the rhizosphere (Hu et al. 2002), while no significant differences existed between C-bonded S in the rhizosphere and in the bulk soil, indicating that C-bonded S may be more important for plant S nutrition (Hu et al. 2003).

Although it is the most bioavailable organic pool in soil, the dissolved fraction typically represents < 1% of the total S pool. For example, dissolved

organic S (DOS) concentrations in soil solutions have been found to range from 143 to 750 $\mu\text{g L}^{-1}$ (Houle et al. 2001; Kaiser and Guggenberger 2005) while levels of extractable organic S have been reported to be much higher (30–60 mg S kg^{-1} ; Wang et al. 2023a) suggesting that a large proportion of the DOS is held electrostatically on soil surfaces. However, the chemical composition of DOS in soil is not well studied. The dominant pool of DOS is a high-molecular-weight pool (rich in humic substances), which is turned over slowly by microorganisms and extracellular enzymes (Jones et al. 2004). The second pool comprises mainly free proteins, peptides, and amino acids; however, it is rapidly turned over by soil microorganisms therefore does not accumulate in soil (Ma et al. 2021a, d; Niknahad-Gharmakher et al. 2012). In sandy agricultural soils with long-term fertilisation, the contents of total S, organic S, microbial biomass S, and SO_4^{2-} were found to be 455, 452, 7.1, and 3.6 mg kg^{-1} , respectively (Ma et al. 2021d). In the case of free amino acids in soil solution, their concentrations in soil are typically very low ($<1 \text{ mg kg}^{-1}$; Jones et al. 2009). In one study, the amount of soluble Cys and Met in soil were found to be only 0.14 and 0.22 mg kg^{-1} , respectively, while the concentration of SO_4^{2-} was much higher, at 1.8 mg kg^{-1} (Ma et al. 2021d). However, even at low concentrations, Cys and Met are in dynamic equilibrium and can be quickly consumed by soil microorganisms and plants (Wang et al. 2023b, c); simultaneously, they are rapidly replenished from the breakdown of proteins and oligopeptides in soil organic matter as well as inputs in the form of root and microbial exudates and atmospheric deposition (Jones et al. 2009; Ren et al. 2017). Due to the rapid turnover of low-molecular-weight organic matter, Cys and Met might represent important sources for replenishing the soil SO_4^{2-} pool and for plant uptake (Ma et al. 2021b). Of clear importance to their functional significance therefore is not just the concentration of the different S solutes but the net flux of these different S forms through the soil solution pool (van Hees et al. 2005).

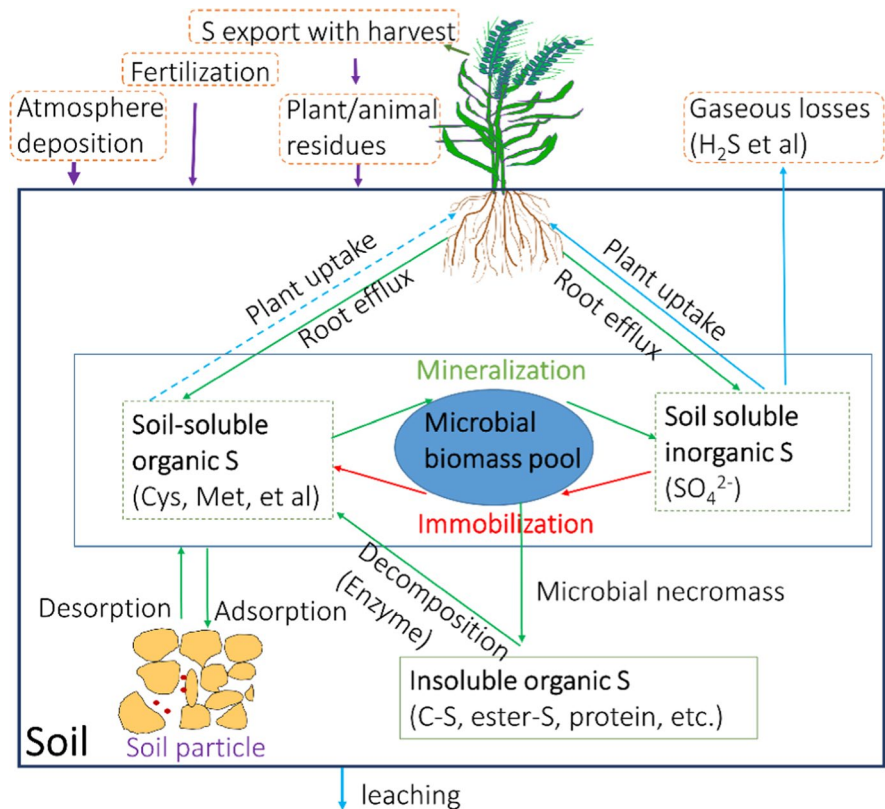
Transformations of S in the soil

Although some organic S is likely to be mineralised abiotically in response to UV irradiation at the soil surface, it is likely that this rate of transformation is very slow (Poulin 2023). Rather, the soil S stock

is subject to myriad of biotic processes, resulting in continuous degradation and re-polymerisation of different forms of S (Fig. 1). Soil S originates from rock weathering, fertilisation, irrigation water, vegetation (i.e., root exudation, plant residues), animal residues and atmospheric deposition, and it can be depleted via plant uptake, gaseous losses, leaching and surface runoff (Ma et al. 2021d; Tanikawa et al. 2014). In soil, S is mainly present in the form of insoluble organic S due to chemical and physical protection on clay surfaces (non-labile organic S), which can be hydrolysed by enzymes to form soil-soluble organic and inorganic S, while the unprotected proportion (labile organic S) is continuously cycled between inorganic and organic forms. Organic S can be decomposed to inorganic S by microorganisms via mineralisation, while inorganic S can be utilised by microorganisms and transformed into large-molecular-weight insoluble organic or soluble organic S via immobilisation (Ma et al. 2021d). Soil organic S can be adsorbed by soil particles due to van der Waals interactions, hydrogen bonding, dipole-dipole interactions, and other electrostatic forces, however, this sorption process is largely unrelated to the presence of S in the compound, being dependent on other functional groups in the organic moiety. Due to their neutral charge in the pH range of most soils, S-containing amino acids are likely to be weakly sorbed to soil particles and thus readily desorbed if the equilibrium with the soil solution changes (Brigatti et al. 1999; Wang et al. 2023b). In contrast, oligopeptides containing S-containing amino acids may be retained strongly on soil particles if they contain positively charged amino acids residues (e.g. lysine). Plants can take up low-molecular-weight organic S intact or inorganic forms derived from them (Chalk et al. 2017; Ma et al. 2020a, c). Despite the importance of S, data on low- and high -molecular-weight organic S transformation/decomposition at the compound-specific level is lacking, along with research on S accumulation in microbial biomass and its release as SO_4^{2-} . Several biogeochemical processes, including Fe and S reactions and microbial mechanisms, were not reported in this review, as this has been extensively reviewed elsewhere (Karimian et al. 2018; Santana et al. 2021).

Organic S mineralisation is crucial for satisfying plant nutrient demand especially in low-sulphate environments (Fakhraee et al. 2017). Approximately

Fig. 1 Schematic representation of the key processes involved in soil sulphur cycling



1–5% of organic S in soil is mineralised within the growing season (Kopittke et al. 2016), with released inorganic SO_4^{2-} available for plant uptake (Ma et al. 2021c). S mineralisation is an important process for plant S nutrition. The average apparent S mineralisation was found to be $36 \text{ kg ha}^{-1} \text{ year}^{-1}$ (18–50 $\text{kg S ha}^{-1} \text{ year}^{-1}$; Carciocchi et al. 2019b). The mineralisation of organic S has been proposed to occur through biological mineralisation (release of inorganic S from C-bonded S following the mineralisation of organic C by microorganisms) and biochemical mineralisation (extracellular hydrolysis of ester-S) (McGill and Cole 1981). The biological mineralization process is driven by the C demand of microorganisms for growth and maintenance, typically releasing inorganic S as a by-product. In the biochemical mineralisation model, the mineralisation of organic S is regulated by the microbial S demand and supply of S, rather than microbial demand for C (energy) (McGill and Cole 1981). In addition, sulfur dioxygenase (EC:1.13.11.18), sulfhydrogenase (EC:1.12.98.4), molybdopterin synthase sulfurtransferase (EC:2.8.1.11), S-L-cysteine hydrolase (EC:3.13.1.6), sulfur reductase (EC:1.12.98.4),

and sulfur-carrier protein adenylyltransferase/sulfurtransferase (EC:2.7.7.80, 2.8.1.11) also play crucial role in soil S cycling (Kertesz 2004; Qi et al. 2021). Arylsulphatases (EC 3.1.6.1) catalyse the hydrolysis of ester-S and can constitute a rate-limiting step in the breakdown of organic matter and soil S cycling (Chen et al. 2019a, b; Cregut et al. 2013). However, as most organic S enters soil via proteins it is likely that aryl-sulfatases play a limited role in S cycling in soil. In this situation we hypothesize that it is the availability of other exoenzymes such as proteases and peptidases that are crucial regulators of organic S cycling in soil. This is supported by studies showing that C-bonded S is a major source of mineralizable S, rather than ester-S in soils; therefore, biological mineralisation is crucial for long-term S mineralisation (Kopittke et al. 2016). In contrast, other studies have highlighted the importance of ester-S for mineralisation (Blum et al. 2013; Kopittke et al. 2016). The process of C-bonded S mineralisation differs from that of ester-S mineralisation (McGill and Cole 1981). It involves a two-step process in which C-bonded S is first converted to ester sulphates, followed by the hydrolysis of the

produced ester sulphates into sulphate (Blum et al. 2013; Dawit et al. 2011; McGill and Cole 1981). Both biological and biochemical processes are essential in S cycling, and their relative importance is attributed to soil S composition and microbial community (Luo et al. 2016). The S cycling rate is controlled by the present microbial community and its metabolic activity, although it is unknown whether this process is controlled by specific genera or microbial species (Kertesz 2004).

The two critical processes in S cycling, the immobilisation of inorganic S and mineralisation of organic S, are both microbially mediated. Inorganic S immobilisation and its incorporation into different S pools has been studied extensively using radio-labelled ^{35}S -sulphate. Based on a soil cultivation test, microbially-mediated SO_4^{2-} uptake was found to continue for up to 96 h, whereas the immobilisation of protein and amino acids occurred over minutes to hours (Ma et al. 2021d). Another study found that soils incorporated 35–44% of ^{35}S -labelled sulphate into organic S within eight weeks (Kertesz 2004). Based on the results of several studies, it is clear that the most rapidly mineralised pool of organic S is one that has been recently immobilised, and that in which mineralisation and immobilisation occur concurrently (Kertesz 2004; Ma et al. 2021d). Sulphate is immobilised into ester-sulphate and converted under microbial action into C-bonded S (Kertesz 2004). C-bound S enters the soil organic S pool through protozoal predation or after the death of soil microorganisms, releasing bacterial and fungi cell compounds into the soil. Furthermore, the immobilisation of SO_4^{2-} is considerably slower than that of amino acids and proteins; this indicates that microorganisms utilise organic S, rather than inorganic S, to satisfy their energy (C) requirement (Ma et al. 2020b). The direct incorporation of amino acids into proteins is also much more energy efficient than taking up and incorporating SO_4^{2-} and NH_4^+ and the *de novo* synthesis of amino acids.

Microbial oxidation of S is an important process where reduced forms of S are present, and involves the microbial oxidation of reduced inorganic S forms (e.g., sulphides, elemental S, thiosulfates) to higher oxidation states (e.g., sulphate). Microbial S oxidation is generally beneficial to alkaline soils in different ways including: (1) increased bioavailability of phosphate, potassium, calcium and magnesium; (2) the acidity produced by oxidation of S can also be

used to lower soil pH and improve alkaline soils especially under warm and wet conditions; (3) the oxidation of elemental S (S^0) has been used as a strategy to reduce nitrate leaching (Kemmitt et al. 2006; Malik et al. 2020). In addition, the oxidation of elemental S will further reduce soil pH in acid soils. An acidified soil environment accelerates the loss of Ca^{2+} and Mg^{2+} . After leaching of Ca^{2+} and Mg^{2+} , the exchange sites on soil particles are replaced by Al^{3+} , which is toxic to most plants under acid conditions (Santana et al. 2021). Although chemical oxidation of S occurs in soils, this process is mainly microbially mediated and largely involves three groups of microorganisms: (1) chemoautotrophic S bacteria (*Thiobacteriaceae*, *Beggiatoaceae* and *Achromatiaceae*); (2) photosynthetic S bacteria (*Thiorhodaceae* and *Chlorobacteriaceae*); and (3) certain heterotrophic microorganisms including some actinomycetes, bacteria and fungi (e.g. *Pseudomonas spp.*, *Arthrobacter spp.*, *Flavobacterium spp.* and *Bacillus spp.*) (Kuenen et al. 1982; Vidyalakshmi et al. 2009). Of these, *Thiobacilli* are chemoautotrophic bacteria who gain energy from oxidising reduced forms of S (Vidyalakshmi et al. 2009). Five species of the genus *Thiobacillus* are regarded as important in S oxidation in soils, viz. *T. denitrificans*, *T. ferrooxidans*, *T. thioparus* and *T. thiooxidans* (Vidyalakshmi et al. 2009).

Sulphate can be directly reduced to sulphide by sulphate reducing bacteria (SRB) via either assimilatory or dissimilatory pathways (Kushkevych et al. 2020). Both assimilatory and dissimilatory reduction of sulphate begin with the activation of sulphate by adenosine triphosphate (ATP). Adenosine phosphosulphate (APS), formed by ATP and sulphate, is then catalysed by the enzyme ATP sulphurylase (Abdulina et al. 2020). In dissimilatory reduction, the sulphate moiety of APS is directly reduced to sulphite (SO_3^{2-}) by the enzyme APS reductase, while in assimilatory reduction, another P atom is added to APS to form phosphoadenosine phosphosulphate (PAPS), PAPS is then reduced to sulphite (Romero et al. 2014). Once sulphite is formed, it is oxidized to sulphide by the enzyme sulphite reductase. The assimilatory pathway generates reduced S compounds for biosynthesis of amino acids and proteins, and therefore does not lead to direct excretion of sulphide (Santana et al. 2021). In contrast, in dissimilatory reduction, sulphate is reduced to inorganic sulphide by obligatory anaerobic sulphate reducing bacteria (Koschorreck 2008). The

conversion of sulphate to H_2S may seem undesirable from a soil fertility perspective, since this process reduce S availability for plant nutrition, but it could be of great significance in soils under alkaline and anaerobic conditions, as the acidity produced through this process can be used to lower soil pH. The predominant SRB genera in soils are *Desulfovibrio*, *Desulfotomaculum* and *Desulfomonas* (Luptakova 2007), all of which excrete the enzymes desulphurases or bisulphate reductase, which are responsible for reduction of S (Meena Singh 2018). The assembly of SRB communities and their relative abundance is highly dependent on soil management regime being strongly related with soil pH and sulphate availability (George et al. 2020).

Soil-soluble protein decomposition

Proteins are a major source of bioavailable organic matter in soil and are an important source of S, N, and C for microorganisms (Tang et al. 2023). However, to become bioavailable to soil microorganisms they first need to be broken down extracellularly into oligopeptides and/or amino acids prior to uptake (Jan et al. 2009). As microbes and plants contain thousands of proteins, they represent a diverse group of organic compounds, differing in their size, charge, structure, and solubility (Ramrez-Sanchez et al. 2016). Some proteins are highly bioavailable, being hydrolysed into polypeptides and amino acids catalysed by proteases and rapidly decomposed by microorganisms (Greenfield et al. 2020). Therefore, determining the mechanism of protein mineralisation in soil is key for modelling and understanding the cycling of soil elements (Greenfield et al. 2020). In soil, soluble proteins account for about 50% of the total soluble organic matter, whereas soluble amino acids account for less than 5% (Greenfield et al. 2018; Näsholm et al. 2010). Although the protein content exceeds the amino acid content in soils, the bioavailability and decomposition rates of proteins are much lower than those of amino acids (Jan et al. 2009). Amino acid decomposition in soils is very rapid, usually occurring in less than 3 h (Farrell et al. 2014; Jones et al. 2009; Ma et al. 2021b), while insoluble proteins decompose at a much slower rate over days to months. Contrary to expectation, recent studies found that the rate of soluble protein mineralisation is nearly as fast as that reported for amino acid turnover;

therefore, proteins may play a crucial role in S cycling (Greenfield et al. 2020; Ma et al. 2021b).

Based on the use of ^{35}S -labelled proteins extracted from plant tissue, the mechanism of protein decomposition has been studied (Ma et al. 2021b). S in proteins is involved in three important processes in soil cycling, including the (1) immobilisation of protein-S into microbial biomass (MB) within minutes, after which proteins are hydrolysed into peptides and amino acids; (2) the S in MB is released as SO_4^{2-} (the highest release occurred two days, when $50\ \mu\text{M}$ ^{35}S -proteins was added, and approximately half of the S was released as SO_4^{2-} in sandy soil); and (3) the released SO_4^{2-} is reutilised by microorganisms (Fig. 2A). Furthermore, in nature, protein decomposition and input from microbial and plants sources is an ongoing process; hence, these processes are always occurring at any a given time. The half-life of plant-derived ^{35}S -protein decomposing in the soil was found to be less than 8 min (Ma et al. 2021b). As the content of proteins is much higher (by at least one order of magnitude) than that of amino acids in soil, rapid decomposition and high bioavailability of proteins are vital for soil S cycling (Greenfield et al. 2018; Näsholm et al. 2010). Compared with insoluble high-molecular-weight proteins, soluble low-molecular-weight proteins are mineralised by microorganisms at a much faster rate, and the easily decomposed proteins are mainly soluble (Ma et al. 2021b). Soluble proteins have a potentially lower adsorption to the solid phase and relatively high bioavailability due to their high diffusion rates in soil solution. The mineralisation of insoluble proteins, which are also abundant in plant cells (such as membrane proteins, tubulin, and actin) and in soil organic matter, has rarely been investigated; thus, this requires further exploration (Greenfield et al. 2020). However, we expect that the decomposition of high-molecular-weight and insoluble proteins should be much slower than that of soluble proteins.

Soil cysteine- and methionine-derived S, N, and C cycling

S-containing amino acids, Met and Cys, are an essential part of soil-soluble organic S and originate from dead microorganisms and plants, manure, and animal residues. Even with relatively low concentrations, amino acids can be mineralised within

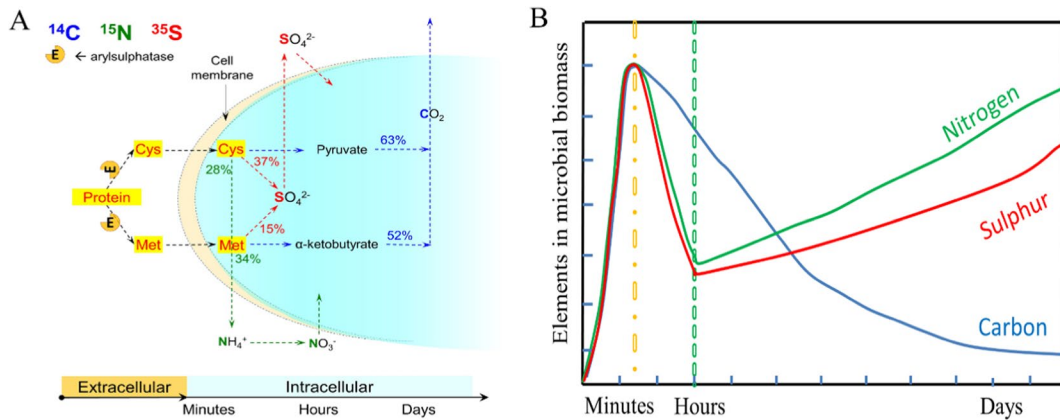


Fig. 2 Cycling mechanisms of carbon (C), nitrogen (N), and sulphur (S) from cysteine (Cys) and methionine (Met) in soil (A) and a simplified model (B). In a sandy textured soil (Woburn), Cys and Met are rapidly immobilised into microbial biomass (MB), and more C is released as CO₂ and S as SO₄²⁻ from Cys than from Met. After microbial uptake, 37% of Cys and only 15% of Met are released as SO₄²⁻ after 3 h. The SO₄²⁻ is then absorbed into the MB, and the ³⁵S-MB contents from Cys and Met reach 61 and 70%, respectively.

Cys and Met release 28 and 34% NH₄⁺, respectively, within 15 min. NH₄⁺ production decreases over time, and some NH₄⁺ oxidises to NO₃⁻. The reduced sulphur moiety (thiol, -SH) in Cys is strongly nucleophilic, rendering it easily transformable to SO₄²⁻. Cys decomposes to pyruvate, NH₄⁺, and H₂S via L-Cys desulphhydrase, and the pyruvate decomposes to CO₂. H₂S oxidises to SO₄²⁻. Met decomposes to α-ketobutyrate, methanethiol (HS-CH₃), and NH₄⁺.

minutes to hours, serving as significant sources of S and N (Hill and Jones 2019; Ma et al. 2021b; Wilkinson et al. 2014). In addition, Cys and Met have been found to be rapidly depleted from freshwater within 1 h (Brailsford et al. 2020). Therefore, Cys and Met are highly bioavailable S and N sources for microorganisms and plant roots, and can be decomposed to SO₄²⁻ and NH₄⁺ by soil microorganisms within minutes, respectively (Ma et al. 2021c, d).

The decomposition of Met and Cys by soil microorganisms involves the rapid immobilisation of amino acids into MB, release of SO₄²⁻, and reutilisation of SO₄²⁻ by soil microorganisms, similar to proteins, but at a faster rate (Ma et al. 2020a, b). As ¹⁴C-, ¹⁵N-, and ³⁵S-labelled Cys and Met are more available than the corresponding labelled proteins, the element cycling of Cys and Met has been intensively explored (Fig. 2). First, they are rapidly immobilised into MB within minutes. Because of the rapid utilisation by microbes, plant roots can only access a limited amount of low-molecular-weight organic S, similar to studies with other amino acids (Jones et al. 2013; Owen and Jones 2001). Second, the S, N, and C in the MB are released in the form of SO₄²⁻, NH₄⁺, and CO₂, respectively (Fig. 2A). Within hours of microbial uptake, a higher ratio of S is released as SO₄²⁻ from Cys than from

Met; however, similar amounts of NH₄⁺ are released (Ma et al. 2021b). NH₄⁺ liberation decreases with time and is partially oxidised to NO₃⁻. NH₄⁺, NO₃⁻, and SO₄²⁻, can be plant-available N and S sources. The disequilibrium between microorganisms and substrates may play important roles in soil S cycling, as a large amount of SO₄²⁻ was released after the uptake of high-S substrates by microorganisms (Ma et al. 2021b). Compared with SO₄²⁻ release from Met, the increased SO₄²⁻ release from Cys can support plant growth as a better S source. As shown in mesocosm studies, wheat and oilseed rape crops utilised 2.6 and 18.7% of the ³⁵S from Cys and only 1.5 and 4.9% of that from Met after 48 h, respectively. The released SO₄²⁻ was then utilised by microorganisms, indicating that microorganisms compete with plants not only for organic S but also for the inorganic S (Ma et al. 2021b, d, 2022a).

The rapid immobilisation of microbial S dominates the gross S fluxes when utilising S-containing amino acids. Following the uptake of the substrate by heterotrophic organisms, the S:C or N:C ratios were found to exceed certain thresholds, resulting in the mineralisation of net S and N as well as the additional release of S and N as SO₄²⁻ and NH₄⁺ to maintain MB stoichiometry, respectively (Ma et al. 2021b;

Manzoni et al. 2017; Mooshammer et al. 2014). In addition, microorganisms retain less S than C from Met and Cys, suggesting that soil organic S mineralisation is driven by a microbial demand for C, similar to organic P mineralisation (Ma et al. 2020b; Spohn et al. 2013). Microbial mineralisation of soil organic S caused by microbial C demand most likely contributes to plant S supply; this might be especially important in soils with low SO_4^{2-} content and low S availability (Fig. 2B). S-containing amino acids decompose rapidly in soil, and SO_4^{2-} release is regulated by inorganic S bioavailability (high SO_4^{2-} in soil stimulates SO_4^{2-} release from Met and Cys). In addition, some of the Met and Cys are adsorbed by soil particles, which might be utilised by plant roots (Cao et al. 2013; Ma et al. 2020a).

Microbial metabolism of organic compounds involves highly controlled catabolic processes that result in NH_4^+ , SO_4^{2-} , and CO_2 release, as well as anabolic processes that result in biomass production (Georgiou et al. 2017; Sinsabaugh et al. 2017). More S and C were retained in MB from Met than from Cys, indicating that the utilisation of microbial elements was strongly controlled by substrate characteristics and quality. This lower proportion of Met utilized in catabolic metabolism could be explained by: (a) Reduced availability of Met to soil microorganisms due to its rapid incorporation into soil organic matter as well as acid labile peptide bonds (Fitzgerald and Andrew 1984); (b) Slower mixing with native soil solution due to its non-polar side chain (Tatko and Waters 2004; Wang et al. 2023c); (c) Production of a variety of biosynthetic intermediates during breakdown (Zhang et al. 2004). An earlier study that used continuous sampling showed that mineralisation was critical for Cys but not for Met (Fitzgerald et al. 1988). Only a small amount of SO_4^{2-} was released, and Met was taken up at relatively high rates by microorganisms (Ma et al. 2021b). The mechanisms of Met and Cys biosynthesis from pyruvate/Cys/oxaloacetate or 3-phosphoglycerate consume 34.3 and 24.7 high-energy phosphate bonds in *Escherichia coli*, respectively (Akashi and Gojobori 2002). Cys decomposition releases less energy than Met decomposition; the latter induces microbial S and C assimilation. The reduced S moiety ($-\text{SH}$, thiol) in Cys is highly nucleophilic and readily decomposes into SO_4^{2-} (Nozaki et al. 2005). We suggest that Cys was decomposed to H_2S , NH_4^+ , and pyruvate

by *L*-Cys desulfhydrase; H_2S was then oxidised into SO_4^{2-} ; pyruvate was decomposed into CO_2 ; Met was found to decompose into methanethiol ($\text{HS}-\text{CH}_3$), NH_4^+ , and α -ketobutyrate (Ma et al. 2021b; Takagi and Ohtsu 2016), and might have been metabolised to *S*-adenosylmethionine, β -thiomethylpropylamine, or α -keto- γ -thiomethylbutyrate (Bustos et al. 2011; Nozaki et al. 2005). However, the activity of the latter processes was likely to be low, as Met released high levels of NH_4^+ (Ma et al. 2021b). SO_4^{2-} release from Met is usually negligible (Fitzgerald and Watwood 1988); it is energetically more efficient for microorganisms to metabolise Met, rather than Cys, to build proteins (Ma et al. 2020b). Specific metabolite detection combined with position-specific isotopic labelling is needed to explore the cycling process thoroughly (Apostel et al. 2015). Such an analysis would provide validation data for the transformation of Met and Cys during various microbial metabolism processes and substrate-regulated morphological changes in soil S, N, and C cycling.

In this review, we focused on S-containing amino acids, proteins, and SO_4^{2-} , rather than other S forms such as NRO-S and C–O–S because the roles of these S forms in soil S cycling remain unclear. In addition, a high concentration of sulphonate C was found in manure derived from the plant-based diet of herbivores. Recently, sulphoquinovose was found in the human gut, where it is an important source of hydrogen sulphide (Hanson et al. 2021). Hence, the cycling of various organic S compounds needs further research.

Plant uptake of S-containing amino acids

Plants take up S from the rhizosphere primarily in the form of SO_4^{2-} and partially as thiosulphate ($\text{S}_2\text{O}_3^{2-}$) against the root's electrochemical potential gradient through the activity of plasma membrane sulphate-specific transporters (Santana et al. 2021), with leaves absorbing a limited amounts of sulphur dioxide (SO_2) (van Der Kooij et al. 1997). In *Arabidopsis thaliana*, the root uptake process is primarily driven by two root-specific high-affinity SO_4^{2-} transporters, SULTR1;2 and SULTR1;1 (Yoshimoto et al. 2010). SO_4^{2-} is absorbed by root cells and transported either into the vacuoles for storage or into the plastids by SULTR;3 transporters (assimilated to organic S compounds). ATP sulfurylase converts SO_4^{2-} to

adenosine 5'-phosphosulfate, which is then phosphorylated to 3'-phosphoadenosine 5'-phosphosulphate or reduced to sulphite (Takahashi et al. 2011). Sulphite is then reduced to sulphide by sulphite reductase, and sulphide is condensed with *O*-acetylserine by *O*-acetylserine(thiol)lyase to form Cys, which can be used as a precursor for Met and glutathione biosynthesis or directly for protein biosynthesis. Met and glutathione biosynthesis can then be used for the biosynthesis of various S-containing derivatives, including phytochelatins and glucosinolates, which are used by plants to detoxify heavy metals and alleviate biotic stress (Cobbett 2000; Liu et al. 2021; Zakari et al. 2021).

Compared to the assimilation of NO_3^- , NH_4^+ and SO_4^{2-} , however, the selective uptake and incorporation of N and S from amino acids via a range of H^+ fuelled amino acid co-transporters may require less energy. Several studies have shown that plants absorb small-molecule organic compounds, such as amino acids (Ganeteg et al. 2017; Jones et al. 2005a; Ma et al. 2017) and quaternary ammonium compounds (Warren 2013). Plants can also absorb large-molecule compounds such as proteins and nucleic acids although the functional significance of this in soil remains unknown (Paungfoolhienne et al. 2008, 2010). Amino acids are highly bioavailable and have high turnover rates (Hill et al. 2011, 2019b; Jones et al. 2018; Jones and Kielland 2012). Cys and Met are important components of low-molecular-weight organic S in soil (Ma et al. 2020c) and can be captured directly by plant roots under hydroponic conditions and from the rhizosphere. A previous study found that potatoes can metabolise large amounts of Cys but not Met (Maggioni and Renosto 1977). According to sterilised hydroponic cultivation (without microbial decomposition) and ^{35}S labelling, oilseed rape, maize and wheat have a great ability to uptake Met and Cys; however, they do not support plant growth at high concentrations ($> 500 \mu\text{M}$), unlike sulphate. The uptake of Met and Cys has been shown to vary between different plant species; for example, uptake by oilseed rape (high S demand) is almost 20 times higher than that by wheat (medium S demand), and the transportation rate is much higher than that of wheat (Ma et al. 2022a, c). This indicates that oilseed rape has a great ability to uptake S-containing amino acids and metabolise and transport them to its shoots.

The uptake of Met and Cys by wheat and oilseed rape increases with S concentration in accordance with Michaelis–Menten kinetics. In contrast, the uptake of sulphate by wheat increases linearly with sulphate concentration (Ma et al. 2022a). The uptake of Cys and Met by wheat is faster than that of sulphate, whereas sulphate uptake by oilseed rape is slower than that of Met but faster than that of Cys. In ^{35}S , ^{15}N , ^{13}C , and ^{14}C quad labelling and pot cultivation tests, crops such as maize, wheat, soybean, and oilseed rape, as well as plants grown in grasslands such as clover, millet, and ryegrass, were shown to utilise only 0.2–2.2% of Cys and Met at low concentrations ($50 \mu\text{M}$) due to: (a) Competition with soil microorganisms and the rapid turnover of Cys and Met by soil microorganisms (Ma et al. 2021c, 2022a, b, c); (b) The lack of transmembrane for amino acids on plant root cells; (c) The relatively high availability of inorganic N and S from soil solution. Wheat and oilseed rape absorbed 0.37–0.81% of intact Cys in the rhizosphere after 6 h. Further evidence for the uptake of organic S by plants can be obtained by detecting added $\text{U-}^{13}\text{C}_5$, ^{15}N -Met in the roots. In the field, wheat and oilseed rape were found to uptake 0.63–2.2% of the added Cys and 0.4–2.1% of the Met, confirming that the plants could capture some of the intact organic S (Ma et al. 2022a). Nevertheless, because soil microbes in well-aerated soils are C-limited, with no significant N or S-limitation, the pressure on plants roots to capture amino acids should be greater than that to capture SO_4^{2-} , NO_3^- , and NH_4^+ (Ma et al. 2021c).

Cys is a superior S source for growth than Met, because it releases more SO_4^{2-} following microbial decomposition. Six hours after microbial absorption, 15.6–33.3% of Met S and 32.5–44.1% of Cys S were found to be transformed into SO_4^{2-} (Ma et al. 2021b). Soybean and maize were found to uptake SO_4^{2-} (85–90% of total S uptake) and inorganic N (98–99%) as their main S and N sources from soil, respectively (Ma et al. 2021c). However, the N from Met and Cys accounted for only approximately 1% of total N uptake from soil, and intact Met and Cys accounted for approximately 0.2% of the total N uptake. This indicates that these two S-containing amino acids play a limited role in plant N nutrition due to the high inorganic N content (primarily from chemical fertilizers) in agricultural soil (Ma et al. 2021c). However, the contributions of Met and Cys to the total

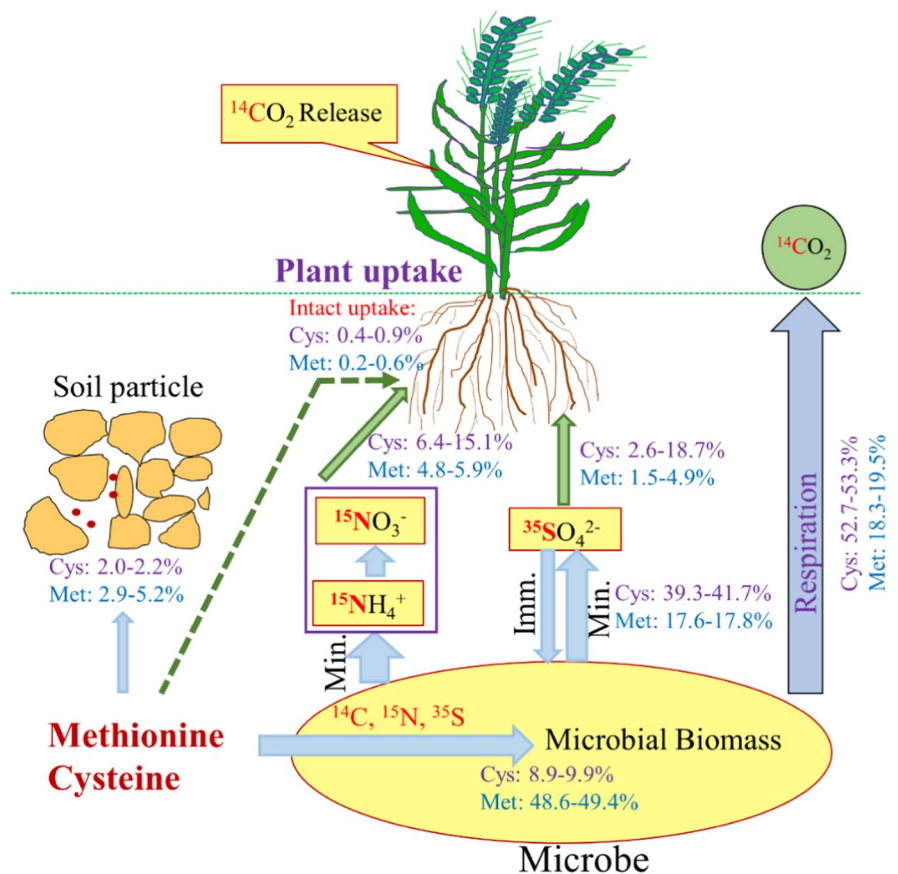
S uptake (10–15%) (that is, organic S and mineral S uptake originating from Met and Cys) were found to be one order of magnitude greater than their contributions to N uptake, suggesting that Cys and Met play important roles in soil S nutrition (Ma et al. 2021c). Overall, we believe that soil S-containing amino acids (Met and Cys) play a limited role in plant N nutrition; however, they are important sources of S for plant growth even at lower concentrations (Ma et al. 2021c) (Fig. 3).

The capture of free amino acids by plants may be maximised by high soil amino acid concentrations (Hill et al. 2019a; Jones et al. 2005b). High transient soil organic S and N concentrations occur after cell death. Following the decomposition of earthworms and clover, amino acid hotspots were found to reach 45.3 and 2.7 mM, respectively, providing high levels of organic S and N for root uptake (Hill et al. 2019b). The decomposition of Met and Cys has been found to be very rapid in soil, decreasing at higher concentrations. The decomposition of soil Cys is rapid (50 μM; $t_{1/2}$ = 1.37 h); however, this rate decreases

with increasing Cys concentrations (1 mM; $t_{1/2}$ = 6.53–6.61 h), indicating that the capture of soil-DOS by plants may occur primarily in soil organic-rich patches (Hill et al. 2019a; Jones et al. 2005b). However, increased amino acids concentrations had little effect on the competition success by either plants or soil micro-organisms in the rhizosphere.

Plants typically compete poorly with soil micro-organisms, as indicated by organic N analysis results (Ganeteg et al. 2017; Kuzyakov and Xu 2013; Ma et al. 2018). The inorganic S and N released during mineralisation create S and N sources for plant roots (Seegmüller and Rennenberg 2002); this suggests that plants can successfully acquire N and S in the long-term due to the unidirectional nutrient flow from soil to roots (Kuzyakov and Xu 2013). Despite fierce competition for nutrients between microorganisms and plants in the rhizosphere, niche differentiation reflects the generation lead time for a mutualistic relationship. This could prevent S and N losses from leaching during periods of slow or no root uptake and

Fig. 3 Simplified model of soil S-containing amino acid cycling (based on rhizo-tube cultivation test using the topsoil (0–10 cm) from an agricultural sandy clay loam textured Eutric Cambisol). After adding to the soil, some of Cys and Met remains in the soil solution. A part of this is absorbed by soil particles, but most of it is immobilised in microbial biomass. The C and S in microbial biomass are released into the soil as CO₂ and SO₄²⁻, respectively; plant roots capture a part of the Cys and Met, and the C they contain is released as CO₂ from leaves. Min.: mineralisation; Imm.: immobilisation



provide roots with continuously available S and N (Kuziyakov and Xu 2013).

Future research

The following aspects should be examined further in future studies:

- 1) Other than proteins and amino acids, the role of soluble organic S forms in plant S nutrition remains unknown. There are various forms of low- and high-molecular-weight organic S; however, their metabolism processes are unknown, and it is unclear whether they can be captured by plant roots under field conditions. Furthermore, due to methodological limitations, it is difficult to detect the long-term amount of organic S uptake; therefore, more research is needed to investigate the contribution of organic S to plant growth.
- 2) Can non-labile organic S be decomposed to sulphate by soil microbes? Which component of insoluble organic S can be decomposed into a soluble form with high bioavailability? Because most soil organic S is insoluble and, thus, inaccessible to soil microorganisms and plant roots, it must be decomposed into a soluble form before it becomes bioavailable. Extensive research is being conducted to determine which parts of insoluble organic S can be readily decomposed and the processes involved.
- 3) The loss of dissolved organic S is vastly understudied. In comparison to sulphate, we know almost nothing about the amount and forms of dissolved and particulate organic S which are lost from soil by runoff and leaching.
- 4) How can we regulate agricultural soil S bioavailability, increase S fertiliser use efficiency, and reduce soil S losses? S fertilisation strategy and soil S management are crucial for crop production and plant growth, both of which require further research. In addition, detailed research on how, when, and where S fertiliser should be applied under different conditions is needed.
- 5) What specific members of microbial community play a dominant role in soil S cycling? It seems likely that particular microbial species or genera in the rhizosphere may play a greater role in S cycling than others, but to date, assays for determining the overall rate of entire metabolic processes such as respiration, or specific enzyme activities do not allow any identification of the specific microbial species directly involved in each measured process. A better understanding of the mechanisms and processes regarding the effects of soil microbes on the availability of nutrients is particularly important for the design of new biofertilizers. The right combination of microbes in these products may enhance the solubility and plant availability of a wide range of different macro- and micro-nutrients (N, P, K and S etc.) making this an economically and environmentally friendly approach to improving plant nutrition (Joshi et al. 2021; Miransari 2013).
- 6) Microbial biomass-S in soil is considered as intermediary between soil inorganic and organic S, and therefore the retention or release of this S pool is vital to support plant growth. Although only a relatively small fraction of the soil organic S resides in microbial biomass-S, this fraction is relatively labile and is thought to be the most active S pool for soil S turnover. Microbial biomass S can form a significant proportion of the organic S pool which is involved in cycling and potentially available to plants (Chapman 1987), and its availability depends on its turnover rate. Therefore, additional studies are particularly needed to improve our understanding of the seasonal variations of microbial biomass S under more soil types with different plant species.
- 7) It is likely that volatile S compounds will be just as important in soils as it is in marine environments (Tang 2020). Sulfurous air pollutants may act as both toxins and nutrients to plants. Atmospheric S gases can be taken up directly by the foliage, forming bisulfite (HSO_3^-) and sulfite (SO_3^{2-}) due to its high solubility in the apoplastic water of the mesophyll (Omasa et al. 2012). Therefore, future studies are needed to assess the magnitude of evolution of volatile S from both soils and plants.

Conclusions

Soil-soluble organic S is essential for soil S cycling, among which soluble S containing proteins and amino acids decompose rapidly. The utilisation of organic S by microorganisms is regulated by substrate characteristics and soil conditions. Plants can utilise limited amounts of intact S-containing amino acids

mainly due to microbial decomposition; therefore, inorganic S derived from amino acid decomposition can be an important S source for plants.

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Data availability Not applicable.

Declarations

Conflict of interest The authors declare that the research was no conflict of any commercial or financial relationships.

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