



Reviews and syntheses: Contribution of sulfate to aerobic methane oxidation in upland soils – a mini-review

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Abstract. Methane (CH₄) is a potent greenhouse gas, and its global warming potential is 28 times higher than carbon dioxide (CO₂). Various environmental factors influence aerobic CH₄ oxidation in soil. The sulfate (SO₄^{2−}) ion is the main component of atmospheric deposition and has been increasing in recent years. It promotes CH₄ production and anaerobic CH₄ oxidation; however, the impact of SO₄^{2−} on aerobic CH₄ oxidation in soils has not yet been comprehensively summarized. We synthesize current research on the effects of SO₄^{2−} on aerobic CH₄ oxidation, examining both its macroscopic manifestations and microscale pathways. Through a literature review, we found that SO₄^{2−} enhances aerobic CH₄ oxidation by 0 %–42 %; moreover, it has been found that various physicochemical properties and processes in the soil are influenced by the addition of SO₄^{2−}, which in turn affects aerobic CH₄ oxidation. This review enhances our understanding of the role of SO₄^{2−} in promoting aerobic CH₄ oxidation. It lays the foundation for future research with two primary goals: (1) validating these findings by quantifying CH₄ flux and aerobic oxidation rates and (2) elucidating the underlying microbial processes through experimental research. Concurrently, the review provides directions for further investigation into the impact of SO₄^{2−} on aerobic CH₄ oxidation.

1 Introduction

Methane (CH₄) is an important greenhouse gas, and its atmospheric concentration has increased since preindustrial times (Place, 2024; Praeg et al., 2016). Its global warming potential is 28 times higher than carbon dioxide (CO₂), owing to its superior heat absorption efficiency (IPCC, 2013). Methanotrophs (aerobic methanotrophs) consume CH₄ under certain conditions (Le Mer and Roger, 2001), reducing the atmospheric CH₄ concentration (Singh et al., 2010). Consequently, methanotrophs are crucial microbes that play an indispensable role in regulating and mitigating the CH₄-related greenhouse effect on Earth. Soil aerobic CH₄ oxidation is the sole known biological sink for atmospheric CH₄ (Ho et al., 2019; Murguía-Flores et al., 2018), contributing to 5 %–7 % of the global annual atmospheric CH₄ uptake (Saunio et al., 2020). Upland soils are the primary biological CH₄ sink (Bodelier, 2011; Guo et al., 2023), owing to methanotroph-mediated CH₄ consumption (Song et al., 2024). This represents the second-largest atmospheric CH₄ consumption sink, surpassed only by hydroxyl radical depletion (Deng et al., 2019). Aerobic CH₄ oxidation in soils is influenced by many factors, such as the soil water content, soil texture, soil type, temperature, soil pH, soil inorganic nitrogen content, and metal availability, and many of these factors have been extensively reviewed (Shukla et al., 2013; Mishra et al., 2018).

However, the effect of SO_4^{2-} , a significant ionic component of acid deposition, on aerobic CH_4 oxidation has not yet been reviewed.

Acid rain, involving the deposition of SO_4^{2-} and other acidic compounds, remains a globally significant environmental issue (Chen et al., 2020; Qi et al., 2022). The three largest affected regions are Europe, North America, and China (Li et al., 2021). SO_4^{2-} is the major ion in acid rain (Wright and Henriksen, 1978) and has profound impacts on substances and biochemical processes in soils. As a crucial component of terrestrial ecosystems, soils serve as the ultimate receptor of acid deposition. SO_4^{2-} deposition induces soil acidification (Huang et al., 2019), alters soil plant diversity (Li et al., 2022), affects microbial properties (Wang et al., 2018), and limits grass yield potential (Klessa et al., 1989), as well as reducing the activities of soil enzymes such as cellulase, invertase, and polyphenol oxidase (Tie et al., 2020). SO_4^{2-} can inhibit CH_4 production (methanogenesis) and promote anaerobic CH_4 oxidation, playing a crucial role in anaerobic CH_4 biogeochemical processes. SO_4^{2-} suppresses methanogenesis, primarily due to its thermodynamic and kinetic preference as an electron acceptor (Granberg et al., 2001; Schimel, 2004), leading to decreased CH_4 emissions (Gauci et al., 2004). SO_4^{2-} has also been shown to facilitate anaerobic CH_4 oxidation by anaerobic methanotrophic archaea in diverse ecosystems, such as oceans (Boetius et al., 2000), wetlands (La et al., 2022), and paddy fields (Fan et al., 2021), acting as a crucial electron acceptor. Despite these well-documented effects on anaerobic CH_4 biogeochemical processes, the influence of SO_4^{2-} on aerobic CH_4 oxidation, particularly in upland soils, remains underexplored. Given the increasing global deposition of SO_4^{2-} due to industrial activities, understanding its impact on aerobic CH_4 oxidation is essential for predicting future CH_4 dynamics and developing effective climate mitigation strategies.

In this review, we have analyzed the literature on the effects of SO_4^{2-} on aerobic CH_4 oxidation. Our analysis not only reveals evidence suggesting that SO_4^{2-} promotes aerobic CH_4 oxidation but also identifies supporting evidence from related studies. In this work, we reviewed references about the influence of SO_4^{2-} on soil properties, substances, or biochemical processes, aiming to elucidate any microscale pathways on aerobic CH_4 oxidation through variations in soil substances or processes. Our analysis reveals that SO_4^{2-} may affect aerobic CH_4 oxidation. Based on the available literature, three out of five studies that investigated the influence of SO_4^{2-} on aerobic CH_4 oxidation were able to demonstrate a positive effect on aerobic CH_4 oxidation thus, we infer that SO_4^{2-} favors aerobic CH_4 oxidation. This review summarizes the microscale pathways by which SO_4^{2-} influences aerobic CH_4 oxidation and highlights the importance of future research in this area. By providing a comprehensive synthesis of existing knowledge, this work serves as a valuable reference for future experimental studies. Furthermore, the find-

ings of this review will contribute to a deeper understanding of global CH_4 cycling, particularly in the context of increasing SO_4^{2-} deposition. Moving forward, we aim to experimentally validate the impact of aerobic CH_4 oxidation following SO_4^{2-} addition and elucidate the underlying microbial mechanisms involved.

2 The microbial aerobic CH_4 oxidation processes

2.1 Aerobic CH_4 oxidation processes

Aerobic CH_4 oxidation is mediated by methanotrophs, a group of specialized microorganisms (Chistoserdova et al., 2005). In soils, aerobic CH_4 oxidation can be classified into two distinct forms based on the concentration of CH_4 (Walsh et al., 2009). The first form, known as high-affinity oxidation, occurs at CH_4 concentrations close to atmospheric levels (< 2 ppm) and is carried out by high-affinity methanotrophs (Chowdhury and Dick, 2013). This process is commonly observed in upland soils, particularly in environments with high NH_4^+ concentrations (Ho et al., 2019; Le Mer and Roger, 2001). The second form, referred to as low-affinity oxidation, occurs at CH_4 concentrations exceeding 40 ppm and is mediated by low-affinity methanotrophs (Chowdhury and Dick, 2013). This form is typically found in wetland environments, where CH_4 concentrations are significantly higher than atmospheric levels (Bechtold et al., 2025). Aerobic CH_4 oxidation converts CH_4 to CO_2 in four steps: ① methane monooxygenase (MMO) oxidizes CH_4 to methanol (CH_3OH), ② methanol dehydrogenase (MDH) oxidizes CH_3OH to formaldehyde (HCHO), ③ formaldehyde dehydrogenase (FADH) oxidizes HCHO to formate (HCOOH), and ④ formate dehydrogenase (FDH) oxidizes HCOOH to CO_2 (Fig. 1, paths ①–④) (Mancinelli, 1995).

2.2 Methanotrophs

Methanotrophs constitute a distinct subset of methylotrophs, primarily dependent on the one-carbon compound CH_4 as their sole source of carbon and energy (Hanson and Hanson, 1996). In the traditional classification system, proteobacterial methanotrophs were categorized into type I (Methylococcaceae and Crenotrichaceae), type II (Methylocystaceae and Beijerinckiaceae), and type X (Methylococcaceae) (Li et al., 2020) based on their cell membrane arrangement, chemotaxonomic properties, physiological characteristics, and phylogenetic locations. However, due to the discovery of non-canonical methanotrophs, the traditional classification system has become outdated. Consequently, methanotrophs are now classified into seven categories based on phylogenetic analysis: types I-A (Methylomonadaceae), I-B (Methylococcaceae), I-C (Methylothermaceae), I-D (Crenotrichaceae), II-A (Methylocystaceae), II-B (Beijerinckiaceae), III (Methylococcaceae), and NC10 (Fenibo et al., 2023). Methylococcaceae, Methylococcaceae, Methylothermaceae, and

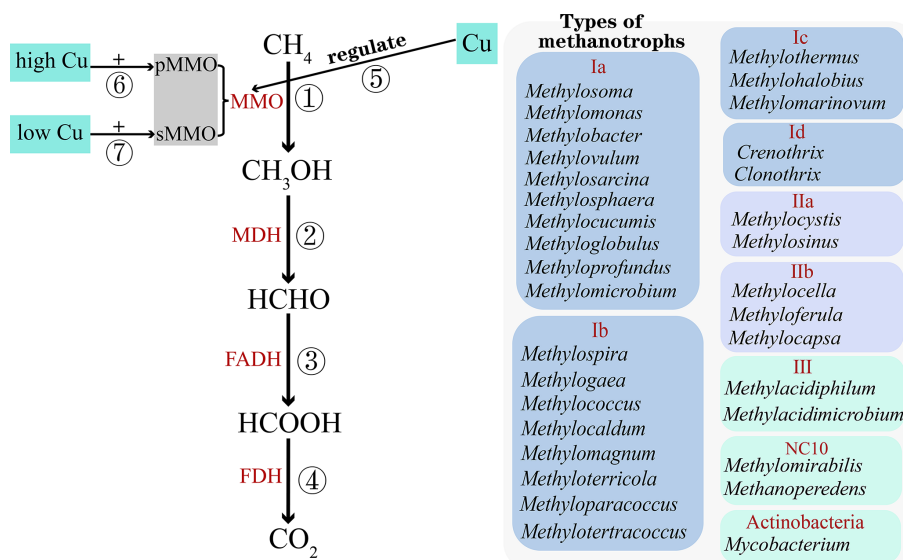


Figure 1. Diagram of the aerobic methane oxidation process and the classification of methanotrophs: ① CH₄ is oxidized to methanol (CH₃OH) by methane monooxygenase (MMO); ② CH₃OH is oxidized to formaldehyde (HCHO) by methanol dehydrogenase (MDH); ③ HCHO is oxidized to formate (HCOOH) by formaldehyde dehydrogenase (FADH); ④ HCOOH is oxidized to CO₂ by formate dehydrogenase (FDH); ⑤ Cu controls two MMOs' expression; ⑥ high Cu concentration regulates pMMO expression in soil; and ⑦ low Cu concentration regulates sMMO expression in soil.

Crenotrichaceae belong to the class Gammaproteobacteria, while Methylocystaceae and Beijerinckiaceae are classified under Alphaproteobacteria. Methylacidiphilaceae belongs to the phylum Verrucomicrobia. The composition of different types of methanotrophs is shown in Fig. 1 (Fenibo et al., 2023). Notably, only four genera – *Methylocella*, *Methylacidimicrobium*, *Methylacidiphilum*, and *Methylomirabilis* – are capable of carbon fixation via the Calvin–Benson–Bassham (CBB) cycle (Fenibo et al., 2023; Op den Camp et al., 2009). Among actinobacterial methanotrophs, *Candidatus Mycobacterium methanotrophicum* is classified with the *Mycobacterium* genus (van Spanning et al., 2022). Methanotrophs utilize two forms of methane monooxygenase (MMO): soluble cytoplasmic monooxygenase (sMMO) and particulate membrane-bound monooxygenase (pMMO). Except for *Methylocella silvestris* and *Methyloferula stellata*, all methanotrophs possess pMMO. sMMO has only been detected in a few specific genera, namely *Methylomonas* sp., *Methylomicrobium* sp., *Methylosinus* sp., and *Methylococcus capsulatus* (DiSpirito et al., 2016). Copper (Cu) concentration differentially regulates MMO expression (Fig. 1 ⑤): high Cu concentrations induces pMMO (Fig. 1 ⑥), whereas low Cu concentrations triggers sMMO (Fig. 1 ⑦) (Hakemian and Rosenzweig, 2007).

3 Soil CH₄ oxidation in response to SO₄^{2−} addition

Sulfates, including SO₄^{2−} and sulfuric acid (H₂SO₄), enhance aerobic CH₄ oxidation within a range of 0 %–42 % (Table 1);

therefore, we hypothesize that SO₄^{2−} may stimulate aerobic CH₄ oxidation. For example, in a temperate mixed deciduous woodland, the cumulative uptake of aerobic CH₄ oxidation was 25 % higher in the experimental group with H₂SO₄ addition compared to the control group during the final quarter of the study period (Bradford et al., 2001b). Similar results were reported by Sitaula et al. (1995). In another study, King and Schnell (1998) found that adding SO₄^{2−} (Na₂SO₄) increased aerobic CH₄ oxidation by 3 % at a CH₄ concentration of 250 ppm compared to the control group, although this result was not statistically significant. The lack of significance may be attributed to the insufficient concentration gradient of Na₂SO₄ in the experimental setup, which limited the ability to fully assess the effects of SO₄^{2−} on aerobic CH₄ oxidation. Therefore, we propose that the observed enhancement of aerobic CH₄ oxidation following H₂SO₄ addition is primarily due to the increase in SO₄^{2−} concentration.

The promotional effect of SO₄^{2−} on aerobic CH₄ oxidation is further supported by comparisons with other anions under similar cationic conditions. Benstead and King (2001) observed that HNO₃ exerted a stronger inhibitory effect on aerobic CH₄ oxidation under equivalent soil acidic conditions than H₂SO₄. This finding is consistent with the results of Bradford et al. (2001a), who experimentally confirmed the inhibitory effect of nitrate (NO₃[−]) on aerobic CH₄ oxidation (Dunfield and Knowles, 1995; Wang and Ineson, 2003). When H₂SO₄ and HNO₃ were added to the soil to achieve H⁺ concentrations of 10 and 1 μmol H⁺ per gram of fresh weight (gfw), respectively, both acids inhibited aerobic CH₄ oxidation to a similar extent. However, H₂SO₄ ex-

Table 1. Promotion effect of sulfates on methane oxidation in diverse upland soils.

Study site	Sulfate concentration	CH ₄ concentration	Effect	Reference
Perridge Forest	H ₂ SO ₄ (50 kg S ha ⁻¹)	Ambient air	25 % increase	Bradford et al. (2001b)
Perridge Forest	H ₂ SO ₄ (5 mM) (NH ₄) ₂ SO ₄ (5 mM)	Ambient air Ambient air	No effect No effect	Bradford et al. (2001a)
Maine forest	Na ₂ SO ₄ (0.5 µg S g ⁻¹ soil)	250 ppm	3 % increase	King and Schnell (1998)
Norway Scots pine forest	H ₂ SO ₄ (pH 3)	Ambient air	42 % increase	Sitaula et al. (1995)
Birch taiga	Na ₂ SO ₄ (2.8 µmol S g ⁻¹ soil) K ₂ SO ₄ (2.8 µmol S g ⁻¹ soil)	4 ppm 4 ppm	No effect No effect	Gulledge and Schimel (1998)

hibited a lesser inhibitory effect than HNO₃. We hypothesize that SO₄²⁻ may promote aerobic CH₄ oxidation, as evidenced by the findings of Benstead and King (2001) and Bradford et al. (2001a).

However, not all studies support the hypothesis that SO₄²⁻ promotes aerobic CH₄ oxidation. For instance, Bradford et al. (2001a) observed no significant difference in aerobic CH₄ oxidation between low (564 µM) and high (1408 µM) concentrations of H₂SO₄ compared to the control group. This discrepancy may be due to differences in H₂SO₄ concentration across studies. Similarly, Hu et al. (2018) reported no significant effect of SO₄²⁻ on aerobic CH₄ oxidation. Based on the available evidence, SO₄²⁻ promotes aerobic CH₄ oxidation within a range of 0 %–42 %. Although the mechanisms by which SO₄²⁻ influences aerobic CH₄ oxidation are not yet fully understood, we have identified potential microscopic pathways through which SO₄²⁻ may affect this aerobic process by reviewing the relevant literature.

4 Microscale pathways by which SO₄²⁻ addition influences aerobic CH₄ oxidation

The impact of SO₄²⁻ on aerobic CH₄ oxidation – particularly its enhancement mechanisms – remains poorly understood. Our literature review identifies two promotive pathways: (i) SO₄²⁻ direct effects on methanotroph activity and community structure (Fig. 2, path d) (Bradford et al., 2001b; Sitaula et al., 1995), thereby modulating CH₄ oxidation; and (ii) SO₄²⁻ indirect effects through alterations in soil physicochemical properties (Fan et al., 2017), substrate availability (Björneras et al., 2019; Palmer et al., 2013; Xu et al., 2017), and nutrient dynamics (Islam, 2012) (Fig. 2), which subsequently influence methanotrophic activity and ultimately affect CH₄ oxidation.

First, the addition of SO₄²⁻ alters soil physicochemical properties (Fig. 2, path a), i.e., particularly by reducing soil pH (Fig. 2 ①). Soil acidification increases due to enhanced base cation leaching associated with SO₄²⁻ addition (Hu et al., 2013), leading to a decrease in the pH of forest soils

(Fasth et al., 1991; Tie et al., 2020). The addition of H₂SO₄ has been shown to promote aerobic CH₄ oxidation by altering the activity or community structure of methanotrophs (Bradford et al., 2001b; Sitaula et al., 1995). However, in experiments involving H₂SO₄ addition, it remains unclear whether the observed enhancement in aerobic CH₄ oxidation is primarily due to the decreased pH (Fig. 2, path e) or the increase in SO₄²⁻ concentration (Fig. 2, path d). Generally, CH₄ consumption is greater under higher-pH conditions in forest soils (Brumme and Borken, 1999; Silver et al., 1999); therefore, the reduction in soil pH may lead to a decrease in aerobic CH₄ oxidation. However, in acidic soils, a decrease in pH has been shown to increase aerobic CH₄ oxidation (Sitaula et al., 1995). Consequently, when evaluating the impact of SO₄²⁻ addition on aerobic CH₄ oxidation, it is essential to consider the initial soil pH (Fig. 2, path e), as methanotrophs exhibit different pH preferences in acidic and alkaline environments (Shukla et al., 2013).

Second, SO₄²⁻ addition can alter the soil microbial substrate (Fig. 2, path b), particularly by decreasing the soil di-O-alkyl C content (Fig. 2 ②) (Xu et al., 2017). In a subtropical forest, SO₄²⁻ addition has been shown to increase the activity of Gram-negative bacteria in soil by reducing the litter di-O-alkyl carbon (di-O-alkyl C) (Fig. 2 ② and path g) (Xu et al., 2017). Di-O-alkyl C is a component of soil organic carbon (SOC). SOC degradation is accelerated when the percentage of di-O-alkyl C is high (Huang et al., 2021); conversely, when the content of di-O-alkyl C is low, SOC degradation slows down, leading to a greater availability of substrates for microorganisms, including methanotrophs. Methanotrophs, which are Gram-negative bacteria (Schimel and Gulledge, 1998), may exhibit increased activity in response to SO₄²⁻ addition. This enhancement of methanotroph activity (Fig. 2, path h) can ultimately promote aerobic CH₄ oxidation (Fig. 2, path o).

Third, SO₄²⁻ can alter the soil nutrition content (Fig. 2, path c), specifically increasing the soil Cu availability (Fig. 2 ③) (Islam, 2012), the phosphorus (P) content (Fig. 2 ④) by enhancing acid phosphatase activity (Lv et al.,

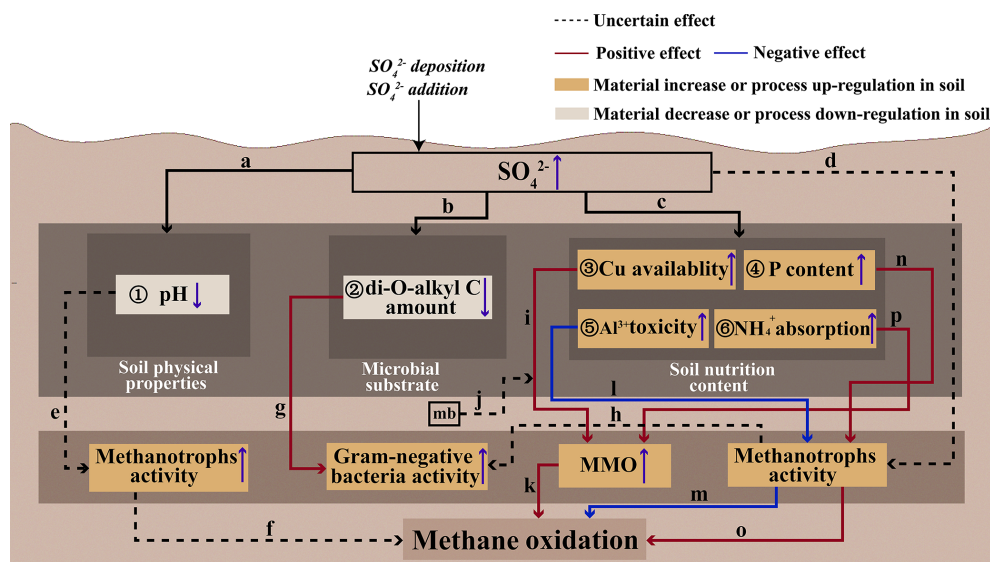


Figure 2. Conceptual diagram of the potential microscopic mechanisms by which sulfate influences aerobic methane oxidation in upland soil: ① SO_4^{2-} decreases soil pH (Fath et al., 1991; Tie et al., 2020); ② SO_4^{2-} decreases the soil di-O-alkyl C amount (Xu et al., 2017); ③ SO_4^{2-} increases soil Cu availability (Islam, 2012); ④ SO_4^{2-} increases the soil P content by increasing soil acid phosphatase activity (Lv et al., 2014; Veraart et al., 2015); ⑤ SO_4^{2-} increases soil Al^{3+} toxicity (Hu et al., 2013; Sogn and Abrahamsen, 1998); ⑥ SO_4^{2-} increases NH_4^+ absorption (Bradford et al., 2001b; Gullledge and Schimel, 1998; King and Schnell, 1998); (a) changes in soil physical properties due to increased soil SO_4^{2-} content; (b) changes in soil microbial substrate due to increased soil SO_4^{2-} content; (c) SO_4^{2-} may promote CH_4 oxidation; (d) SO_4^{2-} affects the activity or community size of methanotrophs in soils (Bradford et al., 2001b; Sitaula et al., 1995); (e) decreased pH may inhibit or stimulate soil CH_4 oxidation (Sitaula et al., 1995); (f) methanotroph activity affects CH_4 oxidation; (g) decreased di-O-alkyl C amount increases soil Gram-negative bacteria activity (Xu et al., 2017); (h) the increased activity of Gram-negative bacteria may stem from the enhanced activity of methanotrophs; (i) elevated Cu availability stimulates soil aerobic CH_4 oxidation (Ho et al., 2013); (j) mb (methanobactin) is expected to accelerate Cu uptake (Knapp et al., 2007); (k) enhanced MMO activity facilitates aerobic CH_4 oxidation. (l) elevated Al^{3+} toxicity inhibits soil methanotroph activity (Nanba and King, 2000; Shukla et al., 2013); (m) decreased methanotroph activity inhibits soil CH_4 oxidation; (n) elevated P content increases soil methanotroph activity (Zhang et al., 2011); (o) elevated methanotroph activity stimulates soil CH_4 oxidation (Bradford et al., 2001b; Sitaula et al., 1995); and (p) the increased adsorption of NH_4^+ enhances the availability of MMO to soil methanotrophs.

2014; Veraart et al., 2015), the Al^{3+} (aluminum ion) toxicity (Fig. 2 ⑤) (Hu et al., 2013; Sogn and Abrahamsen, 1998), and the NH_4^+ absorption (Bradford et al., 2001b; Gullledge and Schimel, 1998; King and Schnell, 1998) (Fig. 2 ⑥). Cu is a crucial component in aerobic CH_4 oxidation processes, with its critical role stemming from its high abundance in catalytically active pMMO complexes – where it directly participates in CH_4 oxidation and facilitates electron transfer from endogenous reductants to molecular oxygen (Balasubramanian and Rosenzweig, 2007; Semrau et al., 2010). This process drives the conversion of CH_4 to methanol (Dassama et al., 2016). It was anticipated that methanobactin secreted by methanotrophs during aerobic CH_4 oxidation would facilitate Cu uptake (Knapp et al., 2007); however, the specific mechanism by which methanobactin affects Cu uptake remains unclear (Fig. 2, path j). For methanotrophs capable of expressing both sMMO and pMMO, the expression of these enzymes is regulated by the availability of Cu, a phenomenon known as the classic “copper switch” (Stanley et al., 1983).

Under Cu-deficient conditions, these methanotrophs express sMMO. However, as the ratio of Cu to biomass increases, the expression of sMMO significantly decreases, while the expression of pMMO increases (Semrau et al., 2018). Notably, nearly all methanotrophs possess pMMO (Koo and Rosenzweig, 2021); therefore, increased Cu availability can enhance the expression of pMMO. Research indicates that Cu can serve as a promoter of aerobic CH_4 oxidation (Ho et al., 2013). Therefore, SO_4^{2-} addition may promote aerobic CH_4 oxidation by increasing the availability of soil Cu, thereby enhancing the expression of pMMO (Fig. 2, path i and k).

A positive correlation has been found between P and aerobic CH_4 oxidation in soils (Veraart et al., 2015; Zhang et al., 2020). P can potentially enhance the activity of soil methanotrophs (Fig. 2, path n) (Zhang et al., 2011), with an increase in soil P content achieved through the hydrolysis of organic compounds, including nucleic acids, phospholipids, and phosphate esters, by acid and alkaline phosphatases (Veraart et al., 2015). The addition of SO_4^{2-} accelerated acid

phosphatase activity, thereby increasing the soil P content (Lv et al., 2014). Therefore, we hypothesize that SO_4^{2-} may indirectly enhance aerobic CH_4 oxidation through the augmentation of soil P content, subsequently promoting the activity of methanotrophs in the soil (Fig. 2, path n and o). It is well established that Al^{3+} inhibits aerobic CH_4 oxidation (Tamai et al., 2007; Tamai et al., 2003). Additionally, soil acidification resulting from SO_4^{2-} addition has been shown to intensify the toxicity of Al^{3+} in forest soils (Fig. 2 ⑤) (Hu et al., 2013; Sogn and Abrahamsen, 1998). The increase in Al^{3+} can inhibit the activity of methanotrophs (Nanba and King, 2000; Shukla et al., 2013) (Fig. 2, path l), thereby inhibiting aerobic CH_4 oxidation (Fig. 2, path m). Therefore, SO_4^{2-} addition may directly affect methanotrophs by enhancing the toxicity of Al^{3+} in the soil, thereby inhibiting aerobic CH_4 oxidation (Fig. 2, path o). When NH_4Cl and $(\text{NH}_4)_2\text{SO}_4$ were added to the soil at the same molar concentration of NH_4^+ , the inhibitory effect of $(\text{NH}_4)_2\text{SO}_4$ on aerobic CH_4 oxidation was weaker than that of NH_4Cl (Adamsen and King, 1993; Bradford et al., 2001a; King and Schnell, 1998). NH_4^+ has been found to inhibit aerobic CH_4 oxidation (Bronson and Mosier, 1994; Dunfield and Knowles, 1995), and the key mechanism is the competition between CH_4 and NH_4^+ for the same MMO enzyme (Gulledge et al., 2004). Due to the similar molecular structures of CH_4 and NH_4^+ , MMO can oxidize both CH_4 (to CH_3OH) and NH_4^+ (to NO_2^-). The inhibitory effect of NH_4Cl is greater than that of $(\text{NH}_4)_2\text{SO}_4$, as SO_4^{2-} may enhance the adsorption of NH_4^+ onto cation exchange sites in the soil (Bradford et al., 2001b; Gulledge and Schimel, 1998; King and Schnell, 1998) (Fig. 2 ⑥). This reduced availability of NH_4^+ limits its ability to compete with methanotrophs for MMO enzymes, thereby increasing the availability of MMO (Fig. 2, path p), promoting aerobic CH_4 oxidation (Fig. 2, path k), and further intensifying the inhibitory effect of NH_4Cl compared to $(\text{NH}_4)_2\text{SO}_4$. In conclusion, SO_4^{2-} served as a facilitator of aerobic CH_4 oxidation, mitigating the inhibitory effects of NH_4^+ on this process.

5 Conclusions

This review synthesizes the double-scale mechanisms by which SO_4^{2-} influences aerobic CH_4 oxidation. Macroscopically, SO_4^{2-} enhances aerobic CH_4 oxidation rates by 0 %–42 %. Mechanistic studies demonstrate that this regulation occurs through SO_4^{2-} -driven alteration of environmental factors (e.g., pH, Cu/P availability, Al^{3+} toxicity, and NH_4^+ absorption), which subsequently modulate methanotroph physiology and MMO activity. Based on synthesized evidence, we hypothesize a net stimulatory effect of SO_4^{2-} on aerobic CH_4 oxidation. Validating this hypothesis requires deeper mechanistic insights; therefore, future research should prioritize quantifying aerobic CH_4 oxidation responses to SO_4^{2-} exposure while elucidating underlying microbial mecha-

nisms. This integrated approach is projected to advance CH_4 mitigation strategies amid rising global SO_4^{2-} deposition.

Data availability. All raw data can be provided by the corresponding authors upon request.

Author contributions. RS finished writing the manuscript; KL, NW, FY, YZ, YS, YZ, LY, and LH gave constructive comments and revised the structure and content of the article; XX and LZ reviewed and edited the manuscript.

Competing interests. The contact author has declared that none of the authors has any competing interests.

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