Contribution of sulfate to aerobic methane oxidation in upland soils: a mini-review

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Abstract. Methane (CH_4) is a potent greenhouse gas, and its global warming potential is 28 times higher than carbon dioxide (CO_2). Various environmental factors influence aerobic CH_4 oxidation in soil. Sulfate (SO_4^{2-}) ion is the main component of atmospheric deposition and has been increasing in recent years. It promotes CH_4 production and anaerobic CH_4 oxidation, however, the impact of SO_4^{2-} on aerobic CH_4 oxidation in soils has not yet been comprehensively summarized. We synthesize current research on the effects of SO_4^{2-} on aerobic CH_4 oxidation, examining both its macroscopic manifestations and microscale pathways. Through a literature review, we found that SO_4^{2-} enhances aerobic CH_4 oxidation by 0–42%, moreover, it has been found that various physicochemical properties and processes in the soil are influenced by the addition of SO_4^{2-}, which in turn affects aerobic CH_4 oxidation. This review enhances our understanding of the role of SO_4^{2-} in promoting aerobic CH_4 oxidation. It lays the foundation for future research with two primary goals: (1) validating these findings by quantifying CH_4 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 SO_4^{2-} on aerobic CH_4 oxidation.

1 Introduction

CH_4 is an important greenhouse gas, and its atmospheric concentration has increased since pre-industrial times (Place, 2024; Praeg et al., 2016). Its global warming potential is 28 times higher than carbon dioxide (CO_2), owing to its superior heat absorption efficiency (IPCC, 2013). Methanotrophs (aerobic methanotrophs) consume CH_4 under certain conditions (Le Mer and Roger, 2001), reducing CH_4 atmospheric concentration (Singh et al., 2010). Consequently, methanotrophs are crucial microbes that play an indispensable role in regulating and mitigating the CH_4-related greenhouse effect on Earth. Soil aerobic CH_4 oxidation is the sole known biological sink for atmospheric CH_4 (Ho et al., 2019; Murguia-Flores et al., 2018), contributing to 5%–7% of the global annual atmospheric CH_4 uptake (Saunois et al., 2020). Upland soils are the primary biological CH_4 sink (Bodelier, 2011; Guo et al., 2023), owing to methanotroph-mediated CH_4 consumption (Song et al., 2024). This represents the second-largest atmospheric CH_4 consumption sink, surpassed only by hydroxyl radical depletion (Deng et al., 2019). Aerobic CH_4 oxidation in soils are influenced by many factors, such as soil water content, soil texture, soil type, temperature, soil pH, soil inorganic nitrogen content, metal availability, etc., 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 ion component of acid deposition, on aerobic CH_4 oxidation has not yet been reviewed.

Acid rain, involving 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 a reduction in 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 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 review, 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, 3 out of 5 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, 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 findings 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 (<2ppm) 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 Robért, 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: ①MMO oxidizes CH_4 to methanol (CH_3OH), ②methanol dehydrogenase (MDH) oxidizes CH_3OH to formaldehyde (HCHO), ③FADH oxidizes HCHO to formate (HCOOH), ④formate 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: Type I-A (*Methylomonadacea*), I-B (*Methylococcaceae*), I-C (*Methylothermaceae*), I-D (*Crenotrichaceae*), II-A (*Methylocystaceae*), II-B (*Beijerinckiaceae*), III (*Methylacidiphilaceae*), and NC10 (Fenibo et al., 2023). *Methylomonadaceae*, *Methylococcaceae*, *Methylothermaceae*, and *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 Figure 1 (Fenibo et al., 2023). Notably, only four genera–*Methylocella*, *Methyacidimicrobium*, *Methylacidiphilum*, and *Methanomirabilis*—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 (MMOs): 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. 1⑥), whereas low Cu concentrations triggers sMMO (Fig. 1⑦) (Hakemian & Rosenzweig, 2007).

3 Soil CH_4 oxidation in response to SO_4^{2-} addition

Sulfates, including SO_4^{2-} and sulfuric acid (H_2SO_4), enhance aerobic CH_4 oxidation within a range of 0–42% (Table 1), so we hypothesize that SO_4^{2-} may stimulate aerobic CH_4 oxidation. For example, in a temperate mixed deciduous woodland, the cumulative uptake of aerobic CH_4 oxidation was 25% higher in the experimental group with H_2SO_4 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 Schell (1998) found that adding SO_4^{2-} (Na_2SO_4) increased aerobic CH_4 oxidation by 3% at a CH_4 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 Na_2SO_4 in the experimental setup, which limited the ability to fully assess the effects of SO_4^{2-} on aerobic CH_4 oxidation. Therefore, we propose that the observed enhancement of aerobic CH_4 oxidation following H_2SO_4 addition is primarily due to the increase in SO_4^{2-} concentration.

The promotional effect of SO_4^{2-} on aerobic CH_4 oxidation is further supported by comparisons with other anions under similar cationic conditions. Benstead and King (2001) observed that HNO_3 exerted a stronger inhibitory effect on aerobic CH_4 oxidation under equivalent soil acidic conditions than H_2SO_4. This finding is consistent with the results of Bradford et al. (2001a), who experimentally confirmed the inhibitory effect of nitrate (NO_3^-) on aerobic CH_4 oxidation (Dunfield and Knowles, 1995; Wang and Ineson, 2003). When H_2SO_4 and HNO_3 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 CH_4 oxidation to a similar extent. However, H_2SO_4 exhibited a lesser inhibitory effect than HNO_3. We hypothesize that SO_4^{2-} may promote aerobic CH_4 oxidation, as evidenced by the findings of Benstead and King (2001) and Bradford et al. (2001a).

However, not all studies support the hypothesis that SO_4^{2-} promotes aerobic CH_4 oxidation. For instance, Bradford et al. (2001a) observed no significant difference in aerobic CH_4 oxidation between low (564 μM) and high (1408 μM) concentrations of

H_2SO_4 compared to the control group. This discrepancy may be due to differences in H_2SO_4 concentration across studies. Similarly, Hu et al. (2018) reported no significant effect of SO_4^{2-} on aerobic CH_4 oxidation. Based on the available evidence, SO_4^{2-} promotes aerobic CH_4 oxidation within a range of 0–42%. Although the mechanisms by which SO_4^{2-} influences aerobic CH_4 oxidation are not yet fully understood, we have identified potential microscopic pathways through which SO_4^{2-} may affect this aerobic process by reviewing relevant literature.

4 Microscale pathways by which SO_4^{2-} addition influences aerobic CH_4 oxidation

SO_4^{2-}'s impact on aerobic CH_4 oxidation—particularly its mechanisms for enhancement—remains unclear. Our literature review reveals two promotion pathways: Shifts in methanotroph activity and community structure (Fig. 2 path d) (Bradford et al., 2001b; Sitaula et al., 1995). Alterations to soil physicochemical properties (Fan et al., 2017), substrate availability (Bjorneras et al., 2019; Palmer et al., 2013; Xu et al., 2017), and nutrient dynamics (Islam, 2012) (Fig. 2).

First, the addition of SO_4^{2-} 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 SO_4^{2-} 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 H_2SO_4 has been shown to promote aerobic CH_4 oxidation by altering the activity or community structure of methanotrophs (Bradford et al., 2001b; Sitaula et al., 1995). However, in experiments involving H_2SO_4 addition, it remains unclear whether the observed enhancement in aerobic CH_4 oxidation is primarily due to the decreased pH (Fig. 2 path e) or the increase in SO_4^{2-} concentration (Fig. 2 path d). Generally, CH_4 consumption is greater at 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 CH_4 oxidation. However, in acidic soils, a decrease in pH has been shown to increase aerobic CH_4 oxidation (Sitaula et al., 1995). Consequently, when evaluating the impact of SO_4^{2-} addition on aerobic CH_4 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, SO_4^{2-} addition can alter the soil microbial substrate (Fig. 2 path b), particularly by decreasing soil di-O-alkyl C content (Fig. 2 ②) (Xu et al., 2017). In a subtropical forest, SO_4^{2-} 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 SO_4^{2-} addition. This enhancement of methanotrophs activity (Fig. 2 path h) can ultimately promote aerobic CH_4 oxidation (Fig. 2 path o).

Third, SO_4^{2-} can alter soil nutrition content (Fig. 2 path c), specifically increasing soil Cu availability (Fig. 2 ③) (Islam, 2012), phosphorus (P) content (Fig. 2 ④) by enhancing acid phosphatase activity (Lv et al., 2014; Veraart et al., 2015), (aluminum ion) Al^{3+} toxicity (Fig. 2 ⑤) (Hu et al., 2013; Sogn and Abrahamsen, 1998), and NH_4^+ absorption (Bradford et al., 2001b; Gulledge 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 &

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 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 $(NH_4)_2SO_4$ were added to the soil at the same molar concentration of NH_4^+, the inhibitory effect of $(NH_4)_2SO_4$ 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 $(NH_4)_2SO_4$, 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 $(NH_4)_2SO_4$. 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, 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 mechanisms. 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 contribution

Rui Su finished writing; Kexin Li, Nannan Wang, Fenghui Yuan, Yunjiang Zuo, Ying Sun, Ying Zhao, Lixin Yang, and Liyuan He gave constructive comments and revised the structure and content of the article; Xiaofeng Xu and Lihua Zhang reviewed and edited the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

Acknowledgments

This study was partially supported by the National Natural Science Foundation of China (32471777; 32271681) and the Joint Funds of China's National Natural Science Foundation (U2006215), and by Academic Team Leadership Program (2024XSYL01), Minzu University of China and by the Major Program of the National Natural Science Foundation of China (42494823), the National Key Research and Development Program of China (2024YFF0808703), the Young Scientists Innovation Funds of State Key Laboratory of Black Soils Conservation and Utilization (2023HTDGZ-QN-03). X.X. acknowledged the financial assistance provided by the National Science Foundation (2145130) and SPRUCE and NGEE Arctic projects, supported by the Office of Biological and Environmental Research in the Department of Energy Office of Science.

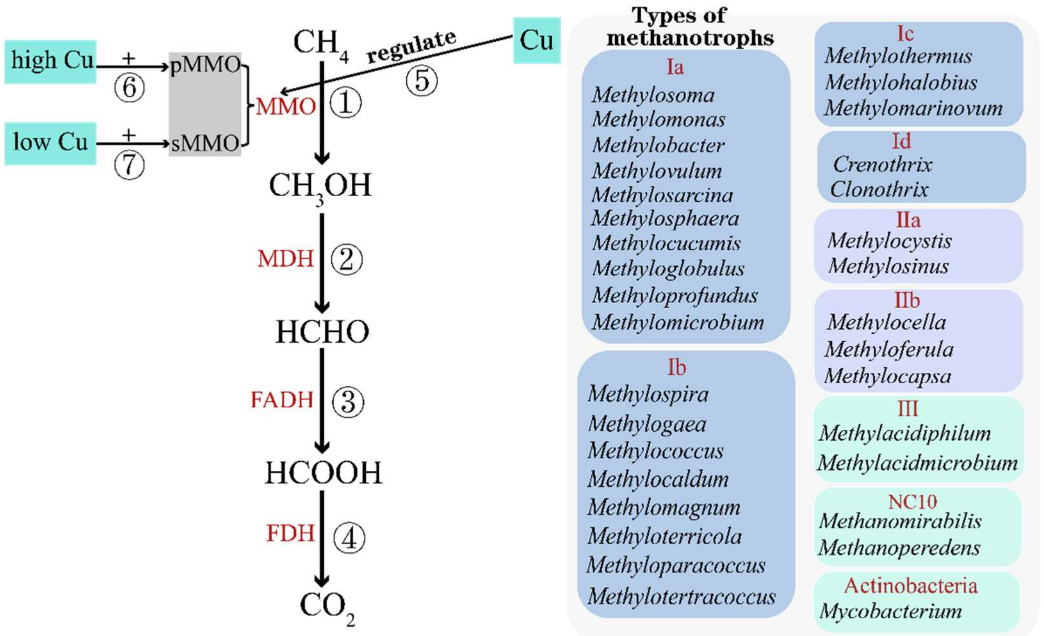

Figure 1: Diagram of the aerobic methane oxidation process, and classification of methanotrophs.

① CH_4 is oxidized to methanol (CH_3OH) by MMO; ② CH_3OH is oxidized to formaldehyde (HCHO) by methanol dehydrogenase (MDH); ③HCHO is oxidized to formate (HCOOH) by formaldehyde dehydrogenase (FADH); ④HCOOH is oxidized to CO_2 by formate dehydrogenase (FDH); ⑤Cu controls two MMOs expression; ⑥ High Cu concentration regulates pMMO expression in soil; ⑦Low Cu concentration regulates sMMO expression in soil.

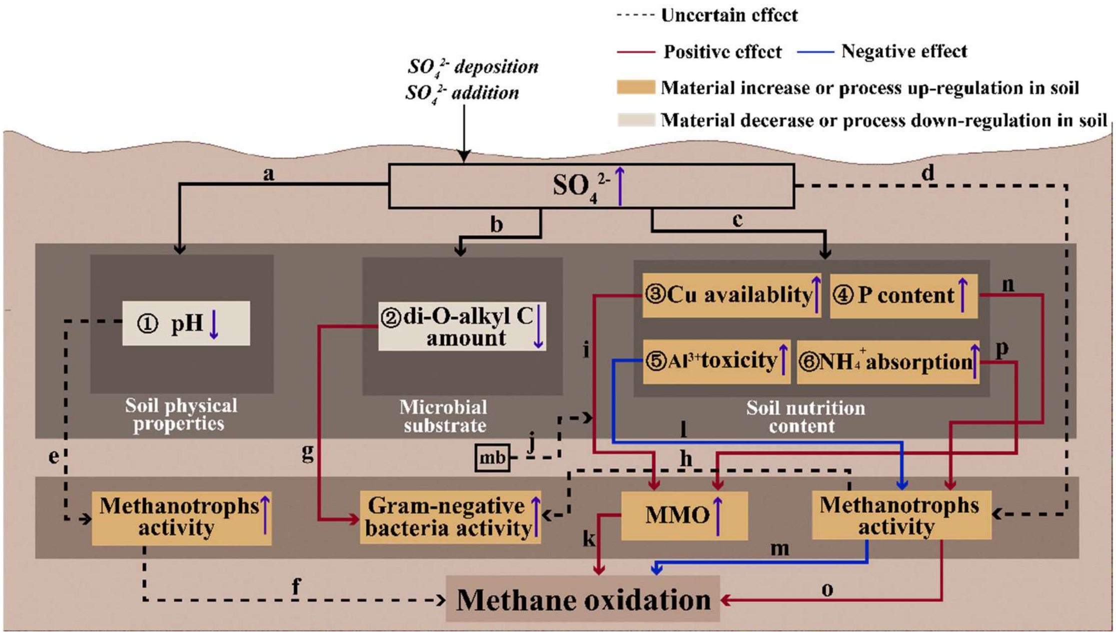

Figure 2. Conceptual diagram of the potential microscopic mechanisms by which sulfate influences aerobic methane oxidation in upland soil.

①SO_4^{2-} decreases soil pH (Fasth et al., 1991; Tie et al., 2020);②SO_4^{2-} decreases soil di-O-alkyl C amount (Xu et al., 2017);③SO_4^{2-} increases soil Cu availability (Islam, 2012); ④SO_4^{2-} increases soil P content by increasing soil acid phosphatase activity (Lv et al., 2014; Veraart et al., 2015); ⑤SO_4^{2-} increases soil Al^{3+} toxicity (Hu et al., 2013; Sogn and Abrahamsen, 1998); ⑥SO_4^{2-} increases NH_4^+ absorption (Bradford et al., 2001b; Gulledge 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. Decreased pH may inhibit or stimulate soil CH4 oxidation (Sitaula et al., 1995); 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 methanotrophs activity (Nanba and King, 2000; Shukla et al., 2013); m. Decreased methanotrophs activity inhibits soil CH_4 oxidation. n. Elevated P content increases soil methanotrophs activity (Zhang et al., 2011); o. Elevated methanotrophs activity stimulates soil CH_4 oxidation (Bradford et al., 2001b; Sitaula et al., 1995); p. The increased adsorption of NH_4^+ enhances the availability of MMO to soil methanotrophs.

Study site	Sulfate concentration	CH_4 concentration	Effect	Reference
Perridge Forest	H_2SO_4 (50 Kg S ha^{-1})	Ambient air	25 % increased	Bradford et al., 2001b
Perridge Forest	H_2SO_4 (5mM)	Ambient air	no effect	Bradford et al., 2001a
	$(NH_4)_2SO_4$ (5mM)	Ambient air	no effect	
Maine forest	Na_2SO_4 0.5μg S g^{-1} soil	250ppm	3% increased	King and Schell, 1998
Norway Scots Pine forest	H_2SO_4 pH3	Ambient air	42% increased	Sitaula et al., 1995
Birch taiga	Na_2SO_4 2.8 μmol S g^{-1} soil	4ppm	no effect	Gulledge and Schimel, 1998
	K_2SO_4 2.8 μmol S g^{-1} soil	4ppm	no effect	

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

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