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 25 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 up to 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 and lays the foundation for future studies aimed at validating these findings by quantifying CH_4 flux and oxidation rates, as well as elucidating the underlying microbial processes through experimental research, while also providing directions for further investigation of SO_4^{2-}'s impact 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 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, characterized by the deposition of SO_4^{2-} and other acidic compounds, has been a significant environmental issue (Chen et al., 2020; Qi et al., 2022). 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 the CH_4 cycle. 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 cycling, 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, 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 processes can be further classified into assimilatory and dissimilatory pathways. In the dissimilatory pathways, CH_4 is sequentially oxidized to CO_2 by multiple enzymes (Fig. 1②). (Mancinelli, 1995). In the assimilation pathways, methanotrophs convert formaldehyde, an intermediate product of aerobic CH_4 oxidation, into biomass and other organic compounds mainly through the ribulose monophosphate pathway (RuMP pathway) (Fig. 1③), serine pathway (Fig. 1④), and xylulose monophosphate pathway (XyMP pathway) (Fig. 1①)(Yang et al., 2023).

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 location. 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). The expression of these enzymes is regulated by copper (Cu) concentration (Hakemian and 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), thus, 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 CH4 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). Consequently, when H_2SO_4 and HNO_3 are added to the soil, resulting in equivalent acidic conditions, the inhibitory effect of H_2SO_4 is less pronounced than that of HNO_3.

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

At present, the impact of SO_4^{2-} on aerobic CH_4 oxidation is not fully understood, and its role in this process remains unclear, particularly regarding its potential enhancing effects. To address this knowledge gap, we conducted a literature review focusing on studies involving the addition of SO_4^{2-}. Through this review, we have identified several potential microscopic pathways through which SO_4^{2-} may promote aerobic CH_4 oxidation. One possible pathway involves changes in methanotroph activity and community structure in response to SO_4^{2-} (Fig. 2 path d) (Bradford et al., 2001b; Sitaula et al., 1995). Alternatively, SO_4^{2-} may affect aerobic CH_4 oxidation by altering soil physical properties (Fan et al., 2017), microbial substrates availability (Bjorneras et al., 2019; Palmer et al., 2013; Xu et al., 2017), and soil nutrition content (Islam, 2012) (Fig. 2).

First, the addition of SO_4^{2-} alters soil physical 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 caused by SO_4^{2-} addition 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, as it is utilized by methanotrophs in their molecular machinery, synthesized from metabolized CH_4 through the secretion of methanobactin into the environment. This process facilitates the oxidation 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

SO_4^{2-} plays a pivotal role in global acid deposition, with annual deposition rates ranging from 141.64 ± 120.04 TgS a^{-1} $year^{-1}$ (Gao et al., 2022). By synthesizing the available literature and exploring both its macroscopic effects and microscopic mechanisms, we investigated how SO_4^{2-} affects aerobic CH_4 oxidation. We observed that SO_4^{2-} enhances aerobic CH_4 oxidation by up to 0–42% on a macro scale. At the microscopic mechanism level, SO_4^{2-} can influence methanotrophs or MMO by modulating pH, di-O-alkyl C content, Cu availability, P content, Al^{3+} toxicity, and NH_4^+ absorption, thereby promoting or inhibiting aerobic CH_4 oxidation. Based on these findings, we hypothesize that SO_4^{2-} would promote aerobic CH_4 oxidation. If this hypothesis is validated in the future, it could provide significant benefits for CH_4 mitigation, particularly in the context of increasing global sulfur deposition. Therefore, future research in this field should focus on investigating the response of aerobic CH_4 oxidation and its influencing factors under increasing SO_4^{2-} conditions, as well as clarifying the underlying microbial mechanisms.

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, 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.

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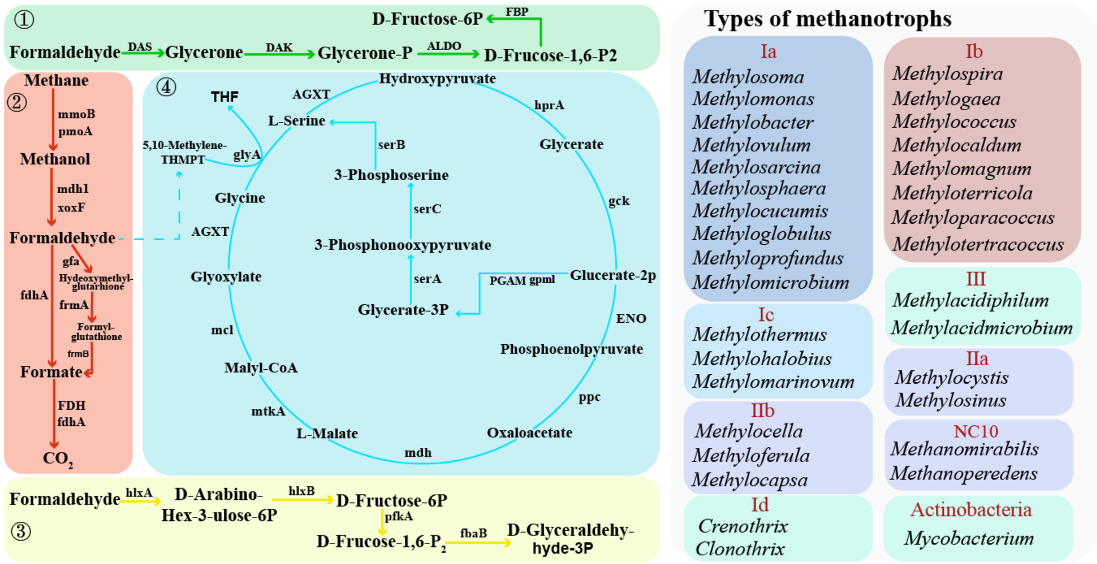

Figure 1: Diagram of the complete aerobic methane oxidation process, including methane assimilation and dissimilation, and classification of methanotrophs.

①Xylulose monophosphate pathway (XyMP pathway) of formaldehyde assimilation; ②CH_4 is oxidized to CO_2 under the sequential action of multiple enzymes; ③Ribulose monophosphate pathway (RuMP pathway)of formaldehyde assimilation; ④Serine pathway of formaldehyde assimilation.

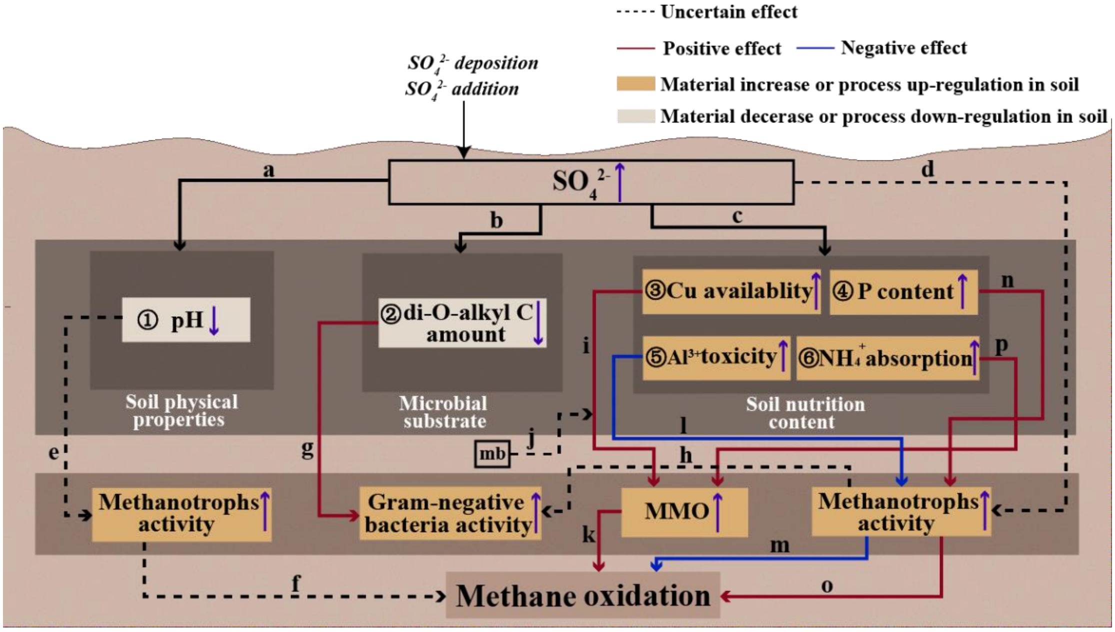

Figure 2. Conceptual diagram of the potential microscopic mechanisms by which sulfate influences aerobic methane oxidation in upland soil.

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.

Reference

Adamsen, A.P.S., King, G.M., Methane consumption in temperate and subarctic forest soils rates, vertical zonation, and responses to water and nitrogen. Applied and Environmental Microbiology 59, 485-490. http://doi.org/10.1128/aem.59.2.485-490.1993, 1993.

Bechtold, E.K., Ellenbogen, J.B., Villa, J.A., Ferreira, D.K.d.M., Oliverio, A.M., Kostka, J.E., Rich, V.I., Varner, R.K., Bansal, S., Ward, E.J., Bohrer, G., Borton, M.A., Wrighton, K.C., Wilkins, M.J., Metabolic interactions underpinning high methane fluxes across terrestrial freshwater wetlands. Nature Communications 16. http://doi.org/10.1038/s41467-025-56133-0, 2025.

Bjorneras, C., Skerlep, M., Floudas, D., Persson, P., Kritzberg, E.S., High sulfate concentration enhances iron mobilization from organic soil to water. Biogeochemistry 144, 245-259. http://doi.org/10.1007/s10533-019-00581-6, 2019.

Bodelier, P.L.E., Interactions between nitrogenous fertilizers and methane cycling in wetland and upland soils. Current Opinion in Environmental Sustainability 3, 379-388. http://doi.org/10.1016/j.cosust.2011.06.002, 2011.

Boetius, A., Ravenschlag, K., Schubert, C., Rickert, D., Widdel, F., Gieseke, A., Amann, R., Jorgensen, B., Witte, U., Pfannkuche, O., A marine microbial consortium apparently mediating anaerobic oxidation of methane. Nature 407, 623-626. http://doi.org/10.1038/35036572, 2000.

Bradford, M.A., Ineson, P., Wookey, P.A., Lappin-Scott, H.M., The effects of acid nitrogen and acid sulphur deposition on CH_4 oxidation in a forest soil: a laboratory study. Soil Biology and Biochemistry 33, 1695-1702. http://doi.org/10.1016/s0038-0717(01)00091-8, 2001a.

Bradford, M.A., Wookey, P.A., Ineson, P., Lappin-Scott, H.M., Controlling factors and effects of chronic nitrogen and sulphur deposition on methane oxidation in a temperate forest soil. Soil Biology and Biochemistry 33, 93-102. http://doi.org/10.1016/S0038-0717(00)00118-8, 2001b.

Bronson, K.F., Mosier, A.R., Suppression of methane oxidation in aerobic soil by nitrogen fertilizers, nitrification inhibitors, and urease inhibitors. Biology and Fertility of Soils 17, 263-268. http://doi.org/10.1007/bf00383979, 1994.

Brumme, R., Borken, W., Site variation in methane oxidation as affected by atmospheric deposition and type of temperate forest ecosystem. Global Biogeochemical Cycles 13, 493-501. http://doi.org/10.1029/1998gb900017, 1999.

Chistoserdova, L., Vorholt, J.A., Lidstrom, M.E., A genomic view of methane oxidation by aerobic bacteria and anaerobic archaea. Genome Biology 6, 1-6. http://doi.org/10.1186/gb-2005-6-2-208, 2005.

Chowdhury, T.R., Dick, R.P., Ecology of aerobic methanotrophs in controlling methane fluxes from wetlands. Applied Soil Ecology 65, 8-22. http://doi.org/10.1016/j.apsoil.2012.12.014, 2013.

Dassama, L.M., Kenney, G.E., Ro, S.Y., Zielazinski, E.L., Rosenzweig, A.C., Methanobactin transport machinery. Proceedings of the National Academy of Sciences of the United States of America 113, 13027-13032. http://doi.org/10.1073/pnas.1603578113, 2016.

Deng, Y., Che, R., Wang, F., Conrad, R., Dumont, M., Yun, J., Wu, Y., Hu, A., Fang, J., Xu, Z., Cui, X., Wang, Y., Upland Soil Cluster Gamma dominates methanotrophic communities in upland grassland soils. Science of the Total Environment 670, 826-836. http://doi.org/10.1016/j.scitotenv.2019.03.299, 2019.

Dunfield, P., Knowles, R., Kinetics of inhibition of methane oxidation by nitrate, nitrite, and ammonium in a humisol. Applied and Environmental Microbiology 61, 3129-3135. http://doi.org/10.1128/aem.61.8.3129-3135.1995, 1995.

Fan, J.L., Xu, Y.H., Chen, Z.M., Xiao, J., Liu, D.Y., Luo, J.F., Bolan, N., Ding, W.X., Sulfur deposition suppressed nitrogen-induced soil N_2O emission from a subtropical forestland in southeastern China. Agricultural and Forest Meteorology 233, 163-170. http://doi.org/10.1016/j.agrformet.2016.11.017, 2017.

Fan, L.C., Schneider, D., Dippold, M.A., Poehlein, A., Wu, W.C., Gui, H., Ge, T.D., Wu, J.S., Thiel, V., Kuzyakov, Y., Dorodnikov, M., Active metabolic pathways of anaerobic methane oxidation in paddy soils. Soil Biology and Biochemistry 156, 108215. http://doi.org/10.1016/j.soilbio.2021.108215, 2021.

Fasth, W.J., David, M.B., Vance, G.F., Sulfate retention and cation leaching of forest soils in response to acid additions. Canadian Journal of Forest Research 21, 32-41. http://doi.org/10.1139/x91-005, 1991.

Fenibo, E.O., Selvarajan, R., Wang, H.Q., Wang, Y., Abia, A.L.K., Untapped talents: insight into the ecological significance of methanotrophs and its prospects. Science of the Total Environment 903, 166145. http://doi.org/10.1016/j.scitotenv.2023.166145, 2023.

Gao, J., Zhou, W., Liu, Y., Sha, L., Song, Q., Lin, Y., Yu, G., Zhang, J., Zheng, X., Fang, Y., Grace, J., Zhao, J., Xu, J., Gui, H., Sinclair, F., Zhang, Y., Litter-derived nitrogen reduces methane uptake in tropical rainforest soils. Science of the Total Environment 849, 157891. http://doi.org/10.1016/j.scitotenv.2022.157891, 2022.

Gauci, V., Matthews, E., Dise, N., Walter, B., Koch, D., Granberg, G., Vile, M., Sulfur pollution suppression of the wetland methane source in the 20th and 21st centuries. Proceedings of the National Academy of Sciences of the United States of America 101, 12583-12587. http://doi.org/10.1073/pnas.0404412101, 2004.

Granberg., G., Sund., I., Svensson., B.H., Nilsson, M., Effect of temperature, and nitrogen and sulfur deposition, on methane emission from a boreal mire. Ecology 82, 1982-1998. 2001.

Gulledge, J., Hrywna, Y., Cavanaugh, C., Steudler, P.A., Effects of long-term nitrogen fertilization on the uptake kinetics of atmospheric methane in temperate forest soils. FEMS Microbiology Ecology 49, 389-400. http://doi.org/10.1016/j.femsec.2004.04.013, 2004.

Gulledge, J., Schimel, J., Low-concentration kinetics of atmospheric CH_4 oxidation in soil and mechanism of NH_4^+ inhibition. Applied and Environmental Microbiology 64, 4291-4298. 1998.

Guo, J.H., Feng, H.L., Peng, C.H., Chen, H., Xu, X., Ma, X.H., Li, L., Kneeshaw, D., Ruan, H.H., Yang, H.Q., Wang, W.F., Global climate change increases terrestrial soil CH_4 emissions. Global Biogeochemical Cycles 37, e2021GB007255. http://doi.org/10.1029/2021gb007255, 2023.

Hakemian, A.S., Rosenzweig, A.C., The biochemistry of methane oxidation. Annual Review of Biochemistry 76, 223-241. http://doi.org/10.1146/annurev.biochem.76.061505.175355, 2007.

Hanson, R.S., Hanson, T.E., Methanotrophic bacteria. Microbiological Reviews 60, 439-471. http://doi.org/10.1128/mmbr.60.2.439-471.1996, 1996.

Ho, A., Lee, H.J., Reumer, M., Meima-Franke, M., Raaijmakers, C., Zweers, H., de Boer, W., Van der Putten, W.H., Bodelier, P.L.E., Unexpected role of canonical aerobic methanotrophs in upland agricultural soils. Soil Biology and Biochemistry 131, 1-8. http://doi.org/10.1016/j.soilbio.2018.12.020, 2019.

Ho, A., Lüke, C., Reim, A., Frenzel, P., Selective stimulation in a natural community of methane oxidizing bacteria: effects of copper on *pmoA* transcription and activity. Soil Biology and Biochemistry 65, 211-216. http://doi.org/10.1016/j.soilbio.2013.05.027, 2013.

Hu, M.J., Wilson, B.J., Sun, Z.G., Huang, J.F., Tong, C., Effects of nitrogen and sulphate addition on methane oxidation in the marsh soil of a typical subtropical estuary (Min River) in China. Chemistry and Ecology 34, 610-623.

http://doi.org/10.1080/02757540.2018.1464153, 2018.

Hu, Y.L., Jung, K., Zeng, D.H., Chang, S.X., Nitrogen- and sulfur-deposition-altered soil microbial community functions and enzyme activities in a boreal mixedwood forest in western Canada. Canadian Journal of Forest Research 43, 777-784. http://doi.org/10.1139/cjfr-2013-0049, 2013.

Huang, J., Zhou, K.J., Zhang, W., Liu, J.X., Ding, X., Cai, X.A., Mo, J.M., Sulfur deposition still contributes to forest soil acidification in the Pearl River Delta, South China, despite the control of sulfur dioxide emission since 2001. Environmental Science and Pollution Research 26, 12928-12939. http://doi.org/10.1007/s11356-019-04831-w, 2019.

Huang, R.L., Crowther, T.W., Sui, Y.Y., Sun, B., Liang, Y.T., High stability and metabolic capacity of bacterial community promote the rapid reduction of easily decomposing carbon in soil. Communications Biology 4, 1376. http://doi.org/10.1038/s42003-021-02907-3, 2021.

IPCC, 2013. Climate change 2013: the physical science basis. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Islam, M., The effect of different rates and forms of sulfur on seed yield and micronutrient uptake by chickpea. Plant, Soil and Environment 58, 399-404. http://doi.org/10.17221/145/2012-pse, 2012.

King, G.M., Schnell, S., Effects of ammonium and non-ammonium salt additions on methane oxidation by Methylosinus trichosporium OB3b and Maine forest soils. Applied and Environmental Microbiology 64, 253-257. 1998.

Klessa, D.A., Frame, J., Golightly, R.D., Harkess, R.D., THE EFFECT OF FERTILIZER SULFUR ON GRASS PRODUCTION FOR SILAGE. Grass and Forage Science 44, 277-281. http://doi.org/10.1111/j.1365-2494.1989.tb02165.x, 1989.

Knapp, C.W., Fowle, D.A., Kulczycki, E., Roberts, J.A., Graham, D.W., Methane monooxygenase gene expression mediated by methanobactin in the presence of mineral copper sources. Proceedings of the National Academy of Sciences of the United States of America 104, 12040-12045. http://doi.org/10.1073/pnas.0702879104, 2007.

Koo, C.W., Rosenzweig, A.C., Biochemistry of aerobic biological methane oxidation. Chemical Society Review 50, 3424-3436. http://doi.org/10.1039/d0cs01291b, 2021.

La, W., Han, X., Liu, C.Q., Ding, H., Liu, M., Sun, F., Li, S., Lang, Y., Sulfate concentrations affect sulfate reduction pathways and methane consumption in coastal wetlands. Water Research 217, 118441. http://doi.org/10.1016/j.watres.2022.118441, 2022.

Le Mer, J., Roger, P., Production, oxidation, emission and consumption of methane by soil: a review. European Journal of Soil Biology 37, 25-50. http://doi.org/10.1016/S1164-5563(01)01067-6, 2001.

Li, C.H., Wang, B., Fang, Z., Yu, H.L., Huang, J.Y., Plant species diversity is driven by soil base cations under acid deposition in desert coal-mining region in northwestern China. Ecological Indicators 145, 109682. http://doi.org/10.1016/j.ecolind.2022.109682, 2022.

Li, Y., Liu, Y.W., Pan, H., Hernández, M., Guan, X.M., Wang, W., Zhang, Q.C., Luo, Y., Di, H.J., Xu, J.M., Impact of grazing on shaping abundance and composition of active methanotrophs and methane oxidation activity in a grassland soil. Biology and Fertility of Soils 56, 799-810. http://doi.org/10.1007/s00374-020-01461-0, 2020.

Lv, Y., Wang, C.Y., Jia, Y.Y., Wang, W.W., Ma, X., Du, J.J., Pu, G.Z., Tian, X.J., Effects of sulfuric, nitric, and mixed acid rain on litter decomposition, soil microbial biomass, and enzyme activities in subtropical forests of China. Applied Soil Ecology 79, 1-9. http://doi.org/10.1016/j.apsoil.2013.12.002, 2014.

Mancinelli, R., The regulation of methane oxidation in soil. Annual Review of Microbiology 49, 581-605. 1995.

Mishra, V.K., Shukla, R., Shukla, P.N., Inhibition of Soil Methane Oxidation by Fertilizer Application: an Intriguing but Persistent Paradigm. Environmental Pollution and Protection 3, 57-69. http://doi.org/10.22606/epp.2018.32001, 2018.

Murguia-Flores, F., Arndt, S., Ganesan, A.L., Murray-Tortarolo, G., Hornibrook, E.R.C., Soil Methanotrophy Model (MeMo v1.0): a process-based model to quantify global uptake of atmospheric methane by soil. Geoscientific Model Development 11, 2009-2032. http://doi.org/10.5194/gmd-11-2009-2018, 2018.

Nanba, K., King, G., Response of atmospheric methane consumption by maine forest soils to exogenous aluminum salts. Applied and Environmental Microbiology 66, 3674-3679. http://doi.org/10.1128/AEM.66.9.3674-3679.2000, 2000.

Op den Camp, H.J., Islam, T., Stott, M.B., Harhangi, H.R., Hynes, A., Schouten, S., Jetten, M.S., Birkeland, N.K., Pol, A., Dunfield, P.F., Environmental, genomic and taxonomic perspectives on methanotrophic *Verrucomicrobia*. Environmental Microbiology Reports 1, 293-306. http://doi.org/10.1111/j.1758-2229.2009.00022.x, 2009.

Palmer, S.M., Clark, J.M., Chapman, P.J., van der Heijden, G.M.F., Bottrell, S.H., Effects of acid sulphate on DOC release in mineral soils: the influence of SO_4^{2-} retention and Al release. European Journal of Soil Science 64, 537-544. http://doi.org/10.1111/ejss.12048, 2013.

Place, S.E., Examining the role of ruminants in sustainable food systems. Grass and Forage Science 79, 135-143. http://doi.org/10.1111/gfs.12673, 2024.

Praeg, N., Wagner, A.O., Illmer, P., Plant species, temperature, and bedrock affect net methane flux out of grassland and forest soils. Plant and Soil 410, 193-206. http://doi.org/10.1007/s11104-016-2993-z, 2016.

Saunois, M., Stavert, A.R., Poulter, B., Bousquet, P., Canadell, J.G., Jackson, R.B., Raymond, P.A., Dlugokencky, E.J., Houweling, S., Patra, P.K., Ciais, P., Arora, V.K., Bastviken, D., Bergamaschi, P., Blake, D.R., Brailsford, G., Bruhwiler, L., Carlson, K.M., Carrol, M., Castaldi, S., Chandra, N., Crevoisier, C., Crill, P.M., Covey, K., Curry, C.L., Etiope, G., Frankenberg, C., Gedney, N., Hegglin, M.I., Hoglund-Isaksson, L., Hugelius, G., Ishizawa, M., Ito, A., Janssens-Maenhout, G., Jensen, K.M., Joos, F., Kleinen, T., Krummel, P.B., Langenfelds, R.L., Laruelle, G.G., Liu, L., Machida, T., Maksyutov, S., McDonald, K.C., McNorton, J., Miller, P.A., Melton, J.R., Morino, I., Muller, J., Murguia-Flores, F., Naik, V., Niwa, Y., Noce, S., Doherty, S.O., Parker, R.J., Peng, C., Peng, S., Peters, G.P., Prigent, C., Prinn, R., Ramonet, M., Regnier, P., Riley, W.J., Rosentreter, J.A., Segers, A., Simpson, I.J., Shi, H., Smith, S.J., Steele, L.P., Thornton, B.F., Tian, H., Tohjima, Y., Tubiello, F.N., Tsuruta, A., Viovy, N., Voulgarakis, A., Weber, T.S., van Weele, M., van der Werf, G.R., Weiss, R.F., Worthy, D., Wunch, D., Yin, Y., Yoshida, Y., Zhang, W., Zhang, Z., Zhao, Y., Zheng, B., Zhu, Q., Zhu, Q., Zhuang, Q., The Global Methane Budget 2000-2017. Earth System Science Data 12, 1561-1623. http://doi.org/10.5194/essd-12-1561-2020, 2020.

Schimel, J., Playing scales in the methane cycle: from microbial ecology to the globe. Proceedings of the National Academy of Sciences of the United States of America 101, 12400-12401. http://doi.org/10.1073/pnas.0405075101, 2004.

Schimel, J., Gulledge, J., Microbial community structure and global trace gases. Global Change Biology 4, 745-758. http://doi.org/10.1046/j.1365-2486.1998.00195.x, 1998.

Semrau, J.D., DiSpirito, A.A., Gu, W., Yoon, S., Metals and Methanotrophy. Applied and Environmental Microbiology 84. http://doi.org/10.1128/aem.02289-17, 2018.

Shukla, P.N., Pandey, K.D., Mishra, V.K., Environmental determinants of soil methane oxidation and methanotrophs. Critical Reviews in Environmental Science and Technology 43, 1945-2011. http://doi.org/10.1080/10643389.2012.672053, 2013.

Silver, W.L., Lugo, A.E., Keller, M., Soil oxygen availability and biogeochemistry along rainfall and topographic gradients in upland wet tropical forest soils. Biogeochemistry 44, 301-328. http://doi.org/10.1007/bf00996995, 1999.

Singh, B.K., Bardgett, R.D., Smith, P., Reay, D.S., Microorganisms and climate change: terrestrial feedbacks and mitigation options. Nature Reviews Microbiology 8, 779-790. http://doi.org/10.1038/nrmicro2439, 2010.

Sitaula, B.K., Bakken, L.R., Abrahamsen, G., CH_4 uptake by temperate forest soil: effect of N input and soil acidification. Soil Biology and Biochemistry 27, 870-880. http://doi.org/10.1016/0038-0717(95)00017-9, 1995.

Sogn, T., Abrahamsen, G., Effects of N and S deposition on leaching from an acid forest soil and growth of Scots pine (Pinus sylvestris L.) after 5 years of treatment. Forest Ecology and Management 103, 177-190. http://doi.org/10.1016/S0378-1127(97)00188-6, 1998.

Song, H., Peng, C., Zhu, Q., Chen, Z., Blanchet, J.-P., Liu, Q., Li, T., Li, P., Liu, Z., Quantification and uncertainty of global upland soil methane sinks: Processes, controls, model limitations, and improvements. Earth-Science Reviews 252. http://doi.org/10.1016/j.earscirev.2024.104758, 2024.

Stanley, S.H., Prior, S.D., Leak, D.J., Dalton, H., COPPER STRESS UNDERLIES THE FUNDAMENTAL CHANGE IN INTRACELLULAR LOCATION OF METHANE MONO-OXYGENASE IN METHANE-OXIDIZING ORGANISMS - STUDIES IN BATCH AND CONTINUOUS CULTURES. Biotechnology

Letters 5, 487-492. http://doi.org/10.1007/bf00132233, 1983.

Tamai, N., Takenaka, C., Ishizuka, S., Water-soluble Al inhibits methane oxidation at atmospheric concentration levels in Japanese forest soil. Soil Biology and Biochemistry 39, 1730-1736. http://doi.org/10.1016/j.soilbio.2007.01.029, 2007.

Tamai, N., Takenaka, C., Ishizuka, S., Tezuka, T., Methane flux and regulatory variables in soils of three equal-aged Japanese cypress (Chamaecyparis obtusa) forests in central Japan. Soil Biology and Biochemistry 35, 633-641. http://doi.org/10.1016/s0038-0717(03)00010-5, 2003.

Tie, L.H., Fu, R., Penuelas, J., Sardans, J., Zhang, S.B., Zhou, S.X., Hu, J.X., Huang, C.D., The additions of nitrogen and sulfur synergistically decrease the release of carbon and nitrogen from litter in a subtropical forest. Forests 11, 1280. http://doi.org/10.3390/f11121280, 2020.

van Spanning, R.J.M., Guan, Q., Melkonian, C., Gallant, J., Polerecky, L., Flot, J.F., Brandt, B.W., Braster, M., Iturbe Espinoza, P., Aerts, J.W., Meima-Franke, M.M., Piersma, S.R., Bunduc, C.M., Ummels, R., Pain, A., Fleming, E.J., van der Wel, N.N., Gherman, V.D., Sarbu, S.M., Bodelier, P.L.E., Bitter, W., Methanotrophy by a Mycobacterium species that dominates a cave microbial ecosystem. Nature Microbiology 7, 2089-2100. http://doi.org/10.1038/s41564-022-01252-3, 2022.

Veraart, A.J., Steenbergh, A.K., Ho, A., Kim, S.Y., Bodelier, P.L.E., Beyond nitrogen: the importance of phosphorus for CH_4 oxidation in soils and sediments. Geoderma 259-260, 337-346. http://doi.org/10.1016/j.geoderma.2015.03.025, 2015.

Walsh, C., O'Regan, B., Moles, R., Incorporating methane into ecological footprint analysis: A case study of Ireland. Ecological Economics 68, 1952-1962. http://doi.org/10.1016/j.ecolecon.2008.07.008, 2009.

Wang, Q., Kwak, J.-H., Choi, W.-J., Chang, S.X., Decomposition of trembling aspen leaf litter under long-term nitrogen and sulfur deposition: effects of litter chemistry and forest floor microbial properties. Forest Ecology and Management 412, 53-61. http://doi.org/10.1016/j.foreco.2018.01.042, 2018.

Wang, Z.P., Ineson, P., Methane oxidation in a temperate coniferous forest soil: effects of inorganic N. Soil Biology and Biochemistry 35, 427-433. http://doi.org/10.1016/s0038-0717(02)00294-8, 2003.

Xu, Y.H., Fan, J.L., Ding, W.X., Gunina, A., Chen, Z.M., Bol, R., Luo, J.F., Bolan, N., Characterization of organic carbon in decomposing litter exposed to nitrogen and sulfur additions: links to microbial community composition and activity. Geoderma 286, 116-124. http://doi.org/10.1016/j.geoderma.2016.10.032, 2017.

Yang, C., Chen, Y.T., Zhang, Q., Qie, X.H., Chen, J.X., Che, Y.J., Lv, D.T., Xu, X.Y., Gao, Y.X., Wang, Z.Y., Sun, J., Mechanism of microbial regulation on methane metabolism in saline–alkali soils based on metagenomics analysis. Journal of Environmental Management 345, 118771. http://doi.org/10.1016/j.jenvman.2023.118771, 2023.

Zhang, L.H., Yuan, F.H., Bai, J.H., Duan, H.T., Gu, X.Y., Hou, L.Y., Huang, Y., Yang, M.G., He, J.S., Zhang, Z.H., Yu, L.J., Song, C.C., Lipson, D.A., Zona, D., Oechel, W., Janssens, I.A., Xu, X.F., Phosphorus alleviation of nitrogen-suppressed methane sink in global grasslands. Ecology Letters 23, 821-830.

http://doi.org/10.1111/ele.13480, 2020.

Zhang, T., Zhu, W., Mo, J., Liu, L., Dong, S., Increased phosphorus availability mitigates the inhibition of nitrogen deposition on CH_4 uptake in an old-growth tropical forest, southern China. Biogeosciences 8, 2805-2813. http://doi.org/10.5194/bg-8-2805-2011, 2011.