Discrepancy in exchangeable and soluble ammonium-induced effects on aerobic methane oxidation: a microcosm study of a paddy soil

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Abstract
Ammonium-induced stimulatory, inhibitory, and/or neutral effects on soil methane oxidation have been attributable to the ammonium concentration and mineral forms, confounded by other edaphic properties (e.g., pH, salinity), as well as the site-specific composition of the methanotrophic community. We hypothesize that this inconsistency may stem from the discrepancy in the cation adsorption capacity of the soil. We postulate that the effects of ammonium on the methanotrophic activity in soil are more accurately portrayed by relating methane uptake rates to the soluble ammonium (bioavailable), rather than the exchangeable (total) ammonium. To reduce adsorption (exchangeable) sites for ammonium in a paddy soil, two successive pre-incubation steps were introduced resulting in a 1000-fold soil dilution (soil enrichment), to be compared to a soil slurry (tenfold dilution) incubation. Ammonium was supplemented as \( \text{NH}_4\text{Cl} \) at 0.5–4.75\( \text{gL}^{-1} \) after pre-incubation. While \( \text{NH}_4\text{Cl} \) significantly stimulated the methanotrophic activity at all concentrations in the soil slurry incubation, methane uptake showed a dose-dependent effect in the soil enrichment. The trend in methane uptake could be explained by the soluble ammonium concentration, which was proportionate to the supplemented ammonium in the soil enrichment. In the soil slurry incubation, a fraction (36–63\%) of the supplemented ammonium was determined to be adsorbed to the soil. Accordingly, \textit{Methylosarcina} was found to predominate the methanotrophic community after the incubation, suggesting the relevance of this methanotroph at elevated ammonium levels (<3.25\( \text{gL}^{-1} \) \( \text{NH}_4\text{Cl} \)). Collectively, our results showed that the soluble, rather than the exchangeable ammonium concentration, is relevant when determining the effects of ammonium on methane oxidation, but this does not exclude other (a)biotic factors concurrently influencing methanotrophic activity.

Keywords Methanotroph · \textit{pmoA} · Ammonium-based fertilization · Wetland agriculture · \textit{Methylosarcina}

Introduction
The effects of ammonium on methane oxidation and the aerobic methanotrophs remain contentious, having been documented to stimulate and inhibit methanotrophic activity in the soil environment, as well as having no apparent effect whereby the ammonium-induced stimulation of methane oxidation is thought to be offset by the adverse effects (e.g., Alam and Jia 2012; Bodelier and Laanbroek 2004; Ji et al. 2020; Krause et al. 2012; Mohanty et al. 2006). Ammonia competitively inhibits methane oxidation, and accumulated products of ammonium oxidation (e.g., nitrite, hydroxylamine) can be toxic to the methanotrophs (Campbell et al. 2011; Nyerger et al. 2010; Nyerger and Stein 2009; Versantvoort et al. 2020). Earlier work showed that ammonium addition impaired methane uptake in soils (King and Schnell 1998; Schnell and King 1994). Paradoxically,
ammonium-based fertilization may also stimulate methane oxidation particularly in agricultural, wetland soils where soil microorganisms compete with crops for limited N sources (e.g., Bodelier et al. 2000; Kaupper et al. 2020a).

The seemingly contradictory effects of ammonium on methane oxidation have been attributable to the dose and mineral forms of ammonium (e.g., ammonium chloride, ammonium sulfate) (Hu and Lu 2015; Krause et al. 2012; Mohanty et al. 2006; Walkiewicz et al. 2018; Xu and Inubushi 2004), as well as the methane concentration (King and Schnell 1998). Besides edaphic properties controlling methane oxidation (Ho et al. 2013a; Kaupper et al. 2020b), the methanotrophs, as well as the non-methanotrophic members of the community, are relevant biotic determinants potentially affecting the response of methane oxidation to external stressors, e.g., high ammonium input (Ho et al. 2020; Kaupper et al. 2020c; 2021; Mohanty et al. 2006). With prior or continuous exposure to ammonium, an ammonium-tolerant methanotrophic community may emerge over time (Ho et al. 2020; Qiu et al. 2008). Typically, the gammaproteobacterial methanotrophs (subgroup type Ia; *Methyllobacter, Methylomonas, Methylosarcina*) are more responsive and show higher N assimilation, benefiting from short-term ammonium availability more than the alphaproteobacterial methanotrophs (subgroup type II; *Methylocystis, Methylosinus*) (Nold et al. 1999; Noll et al. 2008; Yang et al. 2020). Many type II methanotrophs (e.g., *Methylocystis, Methylosinus, Methylocella*), along with specific members of type I (*Methylomonas*), harbor the *nifH* gene (encoding for the nitrogenase), having the potential to fix molecular N and, hence, are competitively superior when N is limited (Graham et al. 1993; Ho and Bodelier 2015). Although canonical aerobic methanotrophs can be broadly grouped into Gammaproteobacteria, Alphaproteobacteria, and Verrucomicrobia based on their biochemistry, physiology, and associated life strategies, methanotrophs show species- and even strain-specific versatility in N metabolism (Ho et al. 2013a; Hoefman et al. 2014; Nyerges and Stein 2009). Therefore, a complex interaction of biotic and abiotic determinants underlies ammonium-induced effects on methane oxidation, which may be site-specific.

Previous studies documented the response of methane oxidation to the total or soluble ammonium after amendment (Table S1). Accordingly, ammonium depletion in soil amendment incubations is often attributed to biological ammonium consumption, which may be a cause for the seemingly contradictory findings given that ammonium (cation) is readily adsorbed to the negatively charged organic matter and soil particles (Ho et al. 2018; King and Schnell 1998). The adsorbed ammonium (non-soluble fraction) may not be fully accessible to soil microorganisms. Therefore, ammonium-induced effects could be misinterpreted in soil incubations, considering the total or exchangeable ammonium concentrations alone. Here, we hypothesized that the apparent inconsistency in ammonium-induced effects on methane oxidation may in part stem from differences in the adsorption capacity of the soil (as determined via the exchangeable and soluble ammonium fractions).

To address our hypothesis, we performed a systematic study using two series of incubations whereby the response in methanotrophic activity, community composition, and abundance in a paddy soil slurry (tenfold dilution) were compared to a soil enrichment (1000-fold dilution) incubation. We anticipate lower adsorption sites for ammonium in the soil enrichment than in the soil slurry incubations. As such, the effects of ammonium will be more accurately reflected in the soil enrichment incubation.

**Materials and methods**

The paddy soil was sampled in May 2015 from the CRA Agricultural Research Council, Rice Research Unit in Verceil, Italy (coordinates, 45° 20’ N, 8° 25’ E). Rice agriculture practice in the sampling site has been described before (Kaupper et al. 2021). After sampling, the soil was air-dried at room temperature and sieved (2 mm) before being stored in a covered plastic container till experimental set up. The soil has a clay texture with a pH of 5.4 and a cation exchange capacity of 6.7 cmol(+)/kg (Cucu et al. 2014). The soil contained a total C and N of 13.9 µg C mg dw−1 and 1.3 µg N mg dw−1, respectively (Ho et al. 2015). Selected nutrient contents include NO₃⁻ (sum of NO₂⁻ and NO₃⁻, total NH₄⁺, and PO₄³⁻ of 34.4 µg dw soil⁻¹, 18.0 µg dw soil⁻¹, and 0.6 µg dw soil⁻¹, respectively (Ho et al. 2015).

In both soil slurry and enrichment incubations, NH₄Cl in ammonium mineral salts (AMS) was supplemented to a final concentration of 0.50 (referred to as treatment 1, T1), 1.25 (T2), 2.00 (T3), 2.50 (T4), 3.25 (T5), and 4.75 g L⁻¹ (T6), corresponding to 9.35, 23.39, 37.42, 46.77, 60.80, and 88.87 mM NH₄⁺, respectively (Fig. S1). In the reference incubation (T0), autoclaved dH₂O, instead of NH₄Cl-supplemented AMS, was added to the soil (Fig. S1). These concentrations were selected based on the effects of NH₄Cl on the methane uptake rates in the same soil (i.e., dose-dependent inhibition of methane uptake was proportional to NH₄Cl concentrations) (Ho et al. 2020). All incubations (n = 3, each treatment) were performed in 120 ml bottles under 2–3%v/v methane in air at 27 °C while shaking (120 rpm) in the dark.

After the incubation, the samples were collected and stored in a –20 °C freezer till DNA extraction for molecular analyses and ammonium and nitrate determination. The methanotrophic abundance and community composition were, respectively, determined by qPCR and Illumina MiSeq sequencing targeting the *pmoA* gene (encoding for
the particulate methane monooxygenase, pMMO). The pmoA gene sequences were deposited at the National Center for Biotechnology Information (NCBI) under the accession number PRJNA691142. The ammonium concentration was determined using standard colorimetric methods as described before (Ho et al. 2020). Exchangeable ammonium, regarded as the total amount of ammonium present, was determined in 2 M KCl (1:2) after filtration (0.22 µm), whereas soluble ammonium was determined in the liquid phase of the soil slurry and enrichment, after centrifugation and filtration (0.22 µm). The soluble ammonium was regarded as the ammonium fraction largely accessible to the microorganisms (bioavailable). The detailed experimental setup and molecular analyses are given in the Supplementary Information.

**Results and discussion**

**Dose-dependent effect of soluble ammonium on methane uptake rates**

Methane was rapidly consumed within 2–3 days after NH₄Cl addition in all the soil slurry incubations (T1–T6) when compared to the reference incubation (T0), where headspace methane decreased by <50%v/v even after 7 days, indicating that supplemented NH₄Cl in AMS stimulated methane uptake rates (Fig. 1a, c). On the other hand, NH₄Cl-induced stimulation of methane uptake was dose-dependent in the soil enrichment (Fig. 1b, d), where the stimulatory effect was significant at <2.50 gL⁻¹ NH₄Cl (T4). Although methane uptake was still detected in the 3.25 and 4.75 gL⁻¹ NH₄Cl-supplemented incubations (T5 and T6), the uptake rates were comparable to the reference (T0) incubation. Therefore, optimum methane uptake occurred at <2.50 gL⁻¹ NH₄Cl in the soil enrichment incubation, whereas the NH₄Cl-induced stimulatory effect in the soil slurry incubation seemingly occurred at all NH₄Cl-supplemented concentrations.

Methane uptake could be related particularly to the soluble ammonium concentration in both soil slurry and enrichment incubations. Soluble ammonium was appreciably lower than the total ammonium concentration in all soil slurry incubations after 5 days, indicating biological ammonium uptake and/or adsorption of a large fraction of the ammonium to the soil (Fig. 2). Considering the relatively little change in the initial total ammonium concentration after the incubation (i.e., total ammonium uptake; Fig. 2a), the appreciably lower soluble ammonium concentration detected is more likely caused by a higher adsorption to the soil than microbially mediated ammonium consumption. To additionally assess the contribution of biological ammonium consumption, future studies could employ isotopically labeled ammonium to track ammonium-derived nitrate (i.e., microbially mediated nitrification) after saturating the soil (and hence, adsorption sites) with unlabeled ammonium. It appears that the supplemented ammonium levels did not reflect on the amounts accessible to the microorganisms, where approximately 36–63% of supplemented ammonium (i.e., difference in the total and soluble ammonium fraction relative to the initial supplemented concentration) was adsorbed to the soil (Fig. 2).

In contrast, soluble ammonium concentrations commensurate with the NH₄Cl-supplemented amount in the soil enrichment incubations (Fig. 2b). Here, at <3.25 gL⁻¹ NH₄Cl (T5), the mean soluble ammonium concentrations after the incubation were lower or comparable to the initial values and were proportionate to the supplemented concentrations (Fig. 2b). In the soil enrichment supplemented with 4.75 gL⁻¹ NH₄Cl (T6), however, ammonium concentration was higher after the incubation, possibly released by lysed cells of organisms adversely affected by the inhibitory ammonium levels. The inhibitory effect was corroborated by the significantly lower methane uptake and methanotrophic abundance when compared to incubations supplemented with lower NH₄Cl concentrations (Figs. 1 and 3). Therefore, methane uptake taken together with the methanotrophic abundance and ammonium concentrations after the soil enrichment incubation indicates that supplemented NH₄Cl was largely accessible to the methanotrophs and could explain the dose-dependent effect on methanotrophic activity (i.e., stimulation at <2.5 gL⁻¹ NH₄Cl and inhibition at 4.75 gL⁻¹ NH₄Cl). Since soluble ammonium concentration was appreciably lower (<1.6 gL⁻¹ NH₄Cl) in all soil slurry incubations, methane uptake was seemingly stimulated, regardless of the supplemented NH₄Cl concentrations (Figs. 1 and 2). Hence, ammonium-induced effects can be influenced by the ion exchange capacity (adsorption/desorption) of the mineral form of ammonium in different soils (King and Schnell 1998). In agreement with our hypothesis, the soluble ammonium, rather than the total ammonium fraction, is relevant to determine ammonium-induced response in methane uptake.

The effects of NH₄Cl addition on the methanotrophic activity may be confounded by other parameters (e.g., AMS-derived copper, salt stress, nitrate, and pH) (DiSpirito et al. 2016; Ho et al. 2013b; 2018; Figs. S2 and S3) during the incubation. Although we cannot completely exclude the effects of these confounding factors, the response in methane uptake appears to be largely induced by the supplemented NH₄Cl in AMS, extended discussion given in the Supplementary Information.
Response of the methanotrophic abundance and community composition to NH₄Cl-AMS amendments

The pmoA gene abundance, which determines the abundance of the methanotrophs, was significantly higher after incubation in T4 to T6 in the soil slurry incubations relative to the reference and starting (after pre-incubation) values (Fig. 3). Although the mean pmoA gene abundance gradually increased in the soil slurry from T1 to T3, the values were not significantly different. On the other hand, the significant increase (p < 0.05) in the pmoA gene abundance (T1 to T4) in the soil enrichment is not consistent with the decreasing methane uptake rates (Figs. 1 and 3). Although statistically significant, the mean pmoA gene abundances in T1 to T4 were within a relatively narrow range (3.5 × 10⁶ to 2.0 × 10⁷ pmoA copy no. ml⁻¹). Admittedly, the DNA-based qPCR analysis may not be as sufficiently sensitive as other biological indicators (e.g., transcript-based analyses) to capture relatively subtle differences, as detected in the activity measurements, likely being obscured by persistent relic DNA in the soil matrix (Carini et al. 2017; Schloter et al. 2018). Nevertheless, the qPCR was effective at capturing more pronounced differences (Ho et al. 2015; Reumer et al. 2018); the severe inhibition in methane uptake rate in T6 is clearly reflected in the appreciably lower mean pmoA gene abundance (1–2 orders of magnitude) when compared to the other treatments in the soil enrichment (Figs. 1d and 3).
Higher relative to the initial pmoA gene abundance (i.e., soil slurry, T4-T6; soil enrichment, T1-T5; Fig. 3). During the soil slurry incubation, the mean pmoA gene abundance increased by 6.7-fold, 10.7-fold, and 13.9-fold, respectively, in T4, T5, and T6, whereas a 22.5-fold, 41.0-fold, 47.0-fold, 134.0-fold, and 48.3-fold increase were detected in the T1, T2, T3, T4, and T5 soil enrichment incubations, respectively. The difference in the pmoA gene abundance (initial and after incubation) indicates methanotrophic growth.

The response of the methanotrophic community composition to the added NH₄Cl was visualized as a principal component analysis (PCA), based on the pmoA gene sequences (Figs. 3 and S4). Notably, introducing two successive pre-incubation steps (Fig. S1) in the soil enrichment altered the composition of the methanotrophs; compared to the soil slurry incubation, methanotrophs belonging to the rice paddy cluster (RPC) decreased in relative abundance in the soil enrichment (Fig. S4). Nevertheless, the predominant methanotrophs in both the soil slurry and enrichment consistently comprised of Methylosarcina (type Ia) and other members of gammaproteobacterial methanotrophs (RPC and other uncultured type Ib methanotrophs), as well as alphaproteobacterial methanotrophs belonging to Methylocystis (type II) (Figs. 3 and S4). These taxa collectively represent >90% of the total methanotrophic population in all incubations. A compositional shift in the methanotrophic community was detected in the soil slurry incubations, whereby Methylosarcina became dominant with increasing NH₄Cl concentrations, diverging from the community in the reference incubation (Fig. 3). Methylosarcina also predominated the population at <3.25 gL⁻¹ NH₄Cl (T5) in the soil enrichment, but community composition in T6 and reference incubations were more similar (Fig. 3).

Methylosarcina was favored in both the soil slurry and enrichment with increasing supplemented NH₄Cl after incubation, despite of the discrepancy in the composition of the methanotrophic community prior to NH₄Cl addition (Figs. 3 and S4). This indicates that NH₄Cl strongly influenced the community composition during the incubation. However, the relative abundance of Methylosarcina decreased in the soil enrichment supplemented with 4.75 gL⁻¹ NH₄Cl (T6), corresponding to significantly lower methanotrophic activity, suggesting that this methanotroph contributed to methane oxidation under moderate NH₄Cl levels (up to 3.25 gL⁻¹, T5). This is not surprising given that gammaproteobacterial methanotrophs of subgroup type Ia are thought to be rapid responders to substrate availability (Ho et al. 2013a; 2017) and would benefit from the sudden availability of extraneous nitrogen sources. Indeed, besides Methylosarcina, other type Ia methanotrophs (e.g., Methylobacter and Methylococcus) have been consistently enriched after ammonium amendments in short-term incubations and showed higher N assimilation (Hu and Lu 2015; Nold et al. 1999; Noll...
et al. 2008; Yang et al. 2020). In line with previous studies (e.g., Alam and Jia 2012; Bodelier et al. 2000; Noll et al. 2008; Qiu et al. 2008), the apparent stimulation of type Ia methanotrophs can be attributable to a relief of N limitation, as indicated by the significant NH₄Cl-induced stimulation (exception, 4.75 g L⁻¹ NH₄Cl in the soil enrichment) of methanotrophic activity.

Contrastingly, an alphaproteobacterial methanotroph, Methylocystis, was enriched in incubations of the same soil where NH₄Cl concentration was increased step-wise from 0.5 to 4.75 g L⁻¹ at 0.25 g L⁻¹ increments (Ho et al. 2020). Because of the prolonged incubation over approximately 3 months with a constantly increasing selection pressure (elevated NH₄Cl concentrations), the predominant
ammonium-tolerant methanotroph that emerged is presumably able to detoxify products of ammonium oxidation (i.e., hydroxylamine, nitrite, nitrate (Ho et al. 2020; López et al. 2019; Versantvoort et al. 2020). Although further oxidation of hydroxylamine and nitrite is not confined to specific methanotroph subgroups (Hoefman et al. 2014; Nyerges and Stein 2009; Poret-Peterson et al. 2008), some Methylocystis appear to be more effective at detoxifying products of ammonium oxidation and hence were relatively more tolerant to ammonium inhibition (Nyerges and Stein 2009). Recently, a hydroxylamine oxidoreductase (responsible for the oxidation of hydroxylamine to nitric oxide) was purified from Methylocystis fumarariolicum SolV, a thermophilic verrucomicrobial methanotroph, but is also likely to occur in other aerobic methanotrophs (Versantvoort et al. 2020). Therefore, different mechanisms may underlie the selection of the gammaproteobacterial (including Methylosarcina) and alphaproteobacterial (including Methylocystis) methanotrophs at high ammonium levels. While a relief of N limitation may favor members of gammaproteobacterial methanotrophs in the short-term as in this study, metabolic capacity to detoxify inhibitory compounds of ammonium oxidation may become relevant over time, determining the fitness and dominance of specific methanotrophs.

Conclusion

We provide a simple, yet plausible reason for the inconsistent documented response of the methanotrophic activity and community composition to ammonium amendment in the soil environment. Our findings do not preclude other (a)biotic determinants occurring concurrently, affecting the response of the methanotrophic activity to ammonium. Not all ammonium will be accessible to the microorganisms. A considerable fraction (36–63%) of the supplemented ammonium can be adsorbed by the soil. Therefore, considering the total ammonium alone may not reflect on the actual ammonium-induced effects on the methanotrophic activity and community composition at the supplemented concentrations. Based on these results, we advocate determining the (i) ammonium fraction that is available to the microorganisms and/or (ii) total ammonium over time, enabling the determination of the baseline ammonium level (i.e., the fraction likely adsorbed to the soil), when documenting ammonium-induced effects on methane uptake. Given that the methanotrophs are differentially affected by the supplemented ammonium, the diversity of the methanotrophs is thus relevant to sustain methanotrophic activity at high ammonium concentrations.

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Declaration

Conflict of interest The authors declare no competing interests.

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