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ORIGINAL ARTICLE

Methanotrophs are favored under hypoxia in ammonium-fertilized soils

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Abstract
Methanotrophy of arable soils is affected by N fertilization, but the knowledge about the effect of oxygen level is poorly understood; soil aeration can fluctuate and zones of low oxygen are widespread in soil. We monitored CH_4 oxidation in three mineral soils (Eutric Cambisol, Haplic Podzol, Mollic Gleysol) under laboratory conditions by varying the O_2 level (from 20 to 2% O_2), with or without NH_4^+ (100 mg N kg^{-1}). In controls (without NH_4^+), CH_4 was oxidized completely in the O_2 range from oxia (20% O_2) to high hypoxia (5% O_2), while the process was inhibited under microoxia (2% O_2). Ammonium application decreased CH_4 consumption in all soils. This negative effect was stronger at 20% and 2% O_2 than under hypoxia. The highest CH_4 oxidation rates and the shortest initial (lag) phases in both control and NH_4^+-amended soils were observed under high (5% O_2) and low (10% O_2) hypoxia.

Keywords Aerobic methane oxidation · Methanotrophic activity · Oxygen level · Ammonium ions · N fertilizers

Introduction

As a greenhouse gas, methane (CH_4) has an important role in global warming. Its concentration has doubled since the industrial age (Kirschke et al. 2013). Soil is a large and dynamic reservoir of C (Amundson 2015) and this ecosystem has great importance in the CH_4 budget. In non-aerated zones, methanogens produce CH_4 (Dubey et al. 2014) but soil has a natural ability to oxidize it due to the activity of aerobic methanotrophic bacteria (Tate 2015). Due to the participation of CH_4 in the global climate change and the mitigating role of methanotrophy in soil, studies on processes responsible for the CH_4 budget are important. In this context, it is particularly important to understand all mechanisms regulating the circulation of CH_4 in soil. Arable soils are generally well aerated (Oenema 2001); therefore, they can be biological sinks for CH_4. However, the methanotrophic activity of soils is controlled by a wide range of factors: CH_4 and O_2 as substrates (Bussmann et al. 2006; Henckel et al. 2000; Hernandez et al. 2015; Li et al. 2015; Mohanty et al. 2016), soil properties and conditions such as organic C content and N availability and moisture, pH and temperature (Einola et al. 2007; Huang et al. 2016; Jäckel et al. 2001; Kravchenko et al. 2005), and human activities, such as grazing, deforestation, and fertilization (Bodelier 2011; Castillo et al. 2017; Chen-rui et al. 2003; Ho et al. 2015; Köster et al. 2017; Trimpler et al. 2016).

Molecular oxygen (O_2) is necessary for cell respiration and plays an important role in several chemical and biochemical processes, including CH_4 oxidation. Since the gas diffusion coefficient declines in water, O_2 availability is influenced by changing soil moisture (Chojnicki et al. 2010; Lamorski et al. 2013). Therefore, it is an important biological driver of greenhouse gas fluxes (Jarecke et al. 2016). Besides, composition of soil air usually differs from that of atmospheric air due to the activity of roots and microorganisms. The average O_2 concentration in soil may be close to the atmospheric value (9.1 mmol O_2 l^{-1}, corresponding to 21% *v*/*v*) (Šantrůčková and Šimek 1994) but hypoxic or anoxic conditions may occur. Therefore, soil aeration usually ranges from 20 to 10% *v*/*v* and can even reach zero (Stępniewski et al. 2005). Especially, microoxic zones with a reduced O_2 concentration between the oxic and anoxic layers are widespread in soil and are natural habitats of bacteria (Morris and Schmidt 2013). Moreover, bacteria with potential for microaerobic metabolism are common in nature due to the widespread occurrence of microoxic zones in many environments. However, there is

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insufficient knowledge about microbial activity in microoxic soil environments (Morris and Schmidt 2013).

Next to O_2, nitrogen (N) is also an important regulator of the activity of methanotrophic bacteria (Gärdenäs et al. 2011), especially in cultivated soil. The contribution of agricultural soils to the total terrestrial area and the increasing use of N fertilizers (Amundson et al. 2015) suggest that the interaction between CH_4 and N becomes important globally in the context of climate change (Bodelier and Steenbergh 2014). Recent studies emphasize that its environmental consequences are not fully recognized. Ammonium can competitively inhibit CH_4 oxidation (Alam and Jia 2012; Bender and Conrad 1995; Dunfield and Knowles 1995; Saari et al. 2004; Steinkamp et al. 2001; Wang and Ineson 2003; Xu and Inubushi 2004; Zheng et al. 2013), but also can stimulate the oxidation (Bodelier et al. 2000; Hu and Lu 2015; Krüger and Frenzel 2003; Rigler and Zechmeister-Boltenstern 1999) or have no effect (Bender and Conrad 1995; Liu et al. 2016). Mineral N turnover is strongly affected by O_2 availability (e.g., nitrification in aerobic conditions, denitrification in anaerobic conditions) (Stępniewski and Stępniewska 2009) and affects the concentrations of soluble N forms (NH_4^+, NO_3^+, NO_2^-) which may affect CH_4 oxidation in soil (Bodelier and Steenbergh 2014). While the effect of NH_4^+ on soil CH_4 oxidation was the focus of previous studies (Bodelier et al. 2000; Saari et al. 2004; Schnell and King 1994), little is known about the effect of O_2, and even less about the effects of the soil type. We hypothesize that the soil O_2 level may be one of the key factors explaining the contrasting results concerning the NH_4^+ effect on methanotrophic activity.

Taking into account the abundance of O_2-deficient zones in soil, we have hypothesized that CH_4 consumption in soil is affected by the O_2 concentration as a result of (1) a direct effect on methanotrophic activity and (2) indirectly, as a consequence of the oxygen-driven microbial transformations, which result in changes in concentrations of soluble N forms (NH_4^+, NO_3^+, NO_2^-). Therefore, our aim was to study methane oxidation in mineral soils under different oxygen levels with or without addition of NH_4^+.

Materials and methods

Soil characteristics

The agricultural soils were Eutric Cambisol, Haplic Podzol, and Mollic Gleysol. Cambisols are the most widespread soil in all EU regions, contributing to about 27% of the land cover area (more than 1.1 mln km^2, including the Eutric Cambisol—about 340,000 km^2) (Tóth et al. 2008). The Haplic Podzol is the most common Podzol (about 401,000 km^2) covering about 14% of the EU area (Tóth et al. 2008). Gleysols represent about 5.3% of the EU soil resources, with the Mollic Gleysol covering about 15,000 km^2 of the land area (Tóth et al. 2008).

The selected soils were characterized by similar particle size distribution, which is important for studies concerning gases diffusion in different soils (Bieganowski et al. 2013; Prajapati and Jacinthe 2014), but differed in the contents of organic C and mineral N forms, and kinetic parameters of CH_4 oxidation assayed under oxic conditions (Table 1). The soils were collected from the surface (0–20 cm), air-dried, sieved to < 2 mm, and stored in shade under dry conditions, at room temperature.

Description of the experiment

In the experiment, CH_4 (1% *v*/*v*) consumption was measured during incubation of the triplicate soil samples (10 g of dry mass in 120-ml glass bottles). The initial oxygen levels were oxia (20% O_2 *v*/*v*), low hypoxia (10% O_2 *v*/*v*), high hypoxia (5% O_2 *v*/*v*), and microoxia (2% O_2 *v*/*v*). Under oxia, we used the atmospheric O_2 concentration; to obtain lower O_2 levels, the headspace of each sample was diluted with pure N_2 and excess air was removed to equilibrate the initial pressure (Walkiewicz et al. 2016). A solution of NH_4Cl was added as

Table 1 Main soil properties (Walkiewicz et al. 2012; Wnuk et al. 2017)

Parameter	Soil type (FAO)		
	Eutric Cambisol	Haplic Podzol	Mollic Gleysol
Location (GPS N coordinates) S	16° 14′ 11.08″ 54° 8′ 44.73″	18° 0′ 35.83″ 52° 38′ 14.4″	19° 43′ 24.76″ 52° 06′ 57.7″
pH (KCl)	6.38	6.50	7.71
C_{org} [%]	1.18	0.43	3.93
N_{tot} [%]	0.08	0.09	0.17
Particle size distribution [%]			
50–2000 μm	71.6	74.6	74.8
2–50 μm	25.1	22.3	21.7
< 2 μm	3.3	3.1	3.5
Texture	Sandy loam	Loamy sand	Loamy sand
Inorganic N [mg N kg^{-1}]			
NH_4^+	4.20	0.49	2.84
NO_3^-	0.74	3.40	5.98
NO_2^-	n.d.	n.d.	n.d.
Macroelements [mg kg^{-1}]			
P	180	30	297
K	93	200	127
Mg	42	25	59
Kinetic parameters of CH_4 oxidation			
K_m [μmol]	5.98	19.79	30.66
V_{max} [μmol g^{-1} h^{-1}]	0.137	0.443	0.55

n.d. not detected

a source of NH_4^+ ions (100 mg N kg^{-1}). Samples without NH_4^+ application but with different initial O_2 concentrations were considered as the controls; they were moistened with distilled water. The investigations were carried out at controlled temperature (25 ± 2 °C, Xu and Inubushi 2009; cooled incubator ST4, Pol-Eko-Aparatura) and at 13–14% *w*/*w* soil moisture corresponding to the field water capacity (pF 2.2) (Walczak et al. 2002). We measured changes in the CH_4 and O_2 concentrations during the 21-day incubation of soil samples.

Gas concentration measurements and soil analysis

The headspace gas was sampled (200 μl), and CH_4 and O_2 consumptions were measured by a gas chromatograph (Shimadzu GC-14A) equipped with a thermal conductivity detector (TCD; temperature 60 °C) and with two columns (3.2-mm diameter), one packed with Porapak Q (for CH_4) and the second packed with Molecular Sieve 5A (for O_2); He was the carrier gas flowing at a rate of 40 cm^{-3} min^{-1}. The temperature of the column was 40 °C (Walkiewicz et al. 2012). The detection limit for CH_4 was 0.002% *v*/*v* and 0.40% *v*/*v* for O_2. The detector responses were calibrated using certified gas standard containing 1% CH_4, 20.9% O_2, 0.5% N_2O, and 77.6% N_2 (Air Products).

Main soil properties were measured in air-dried soils. Organic C (C_{org}) was determined using a TOC-VCPH analyzer (Shimadzu, Japan) (Szarlip et al. 2014), the soil pH level was measured potentiometrically by adding 1 M KCl (1:2.5 *w*/*w*) to soil and after 24-h stabilization at room temperature, and N forms (ammonium, nitrate, nitrite) were analyzed in 0.01 M $CaCl_2$ extracts by flow injection analysis (FIA Star 5000 autoanalyzer, FOSS Tecator). Particle size distribution (PSD) was determined using the laser diffraction method (Dobrowolski et al. 2012) by Mastersizer 2000 (Malvern, UK) with a Hydro G dispersion unit (Sochan et al. 2012). Phosphorus and potassium concentrations were determined by the Egner-Riehm (DL) method, while magnesium concentration was determined by the atomic absorption spectrometry (AAS) (Tkaczyk et al. 2017).

Calculations and statistics

The obtained data include changes in the CH_4 concentration during the incubation. Depending on the initial O_2 concentration, the CH_4 depletion curve could be divided into two phases due to different CH_4 oxidation rates (Bender and Conrad 1992, 1995; Steenbergh et al. 2010): lag phase I (initial) and phase II (induced, final). The CH_4 concentration was expressed as milligram CH_4-C kg^{-1} dry soil. It was corrected for solubility in water using the Bunsen solubility coefficient ($\alpha = 0.029$ dm^3 dm^{-3} at 25 °C). The CH_4 density of 0.657 mg cm^{-3} was used for calculating the gas mass (Gliński and Stępniewski 1985). Based on the CH_4 changes (C—the final, and C_0—the initial CH_4 concentration) during time (t), the average rates of CH_4 oxidation were calculated for all incubation periods using the following equation: CH_4 oxidation rate = $(C\text{-}C_0) / t$ (Wnuk et al. 2017). The equation $C = C_0 e^{-kt}$, where k is the first-order kinetic constant (Mohanty et al. 2016), was used for calculating the half-life value ($t_{1/2}$) expressed as days.

The data were subjected to analysis of variance. To compare the effect of O_2 on CH_4 oxidation rates; we used one-way ANOVA in particular variants and multi-factor MANOVA considering the significance of three factors: (1) soil properties; (2) O_2 level; and (3) NH_4^+ addition (post hoc Tukey test; STATISTICA 10.0 program, StatSoft Inc.).

Results

Methane oxidation in control soils under different oxygen levels

All soils incubated without NH_4^+ addition (controls) consumed CH_4 within 4–9 days under hypoxic (5% and 10% O_2) and within 5–11 days under oxic (20% O_2) conditions with a biphasic pattern. In contrast, strong inhibition and no distinct phases were observed under microoxic conditions (2% O_2) (Fig. 1).

The length of the initial (lag) phase of CH_4 oxidation was affected by soil properties. As a result, the average CH_4 oxidation rate (Fig. 3) ranked as Eutric Cambisol < Haplic Podzol < Mollic Gleysol. The highest values (6 to 15 mg CH_4-C kg^{-1} day^{-1}) were achieved at 5% and 10% O_2 in all tested soils ($p < 0.05$). Under oxia (20% O_2), the CH_4 oxidation was slower, ranging from about 5 to 12 mg CH_4-C kg^{-1} day^{-1} ($p < 0.05$). The lowest values (0.351 to 1.382 mg CH_4 kg^{-1} day^{-1}) were observed under microoxia (2% O_2) in all soils. Therefore, the half-life ($t_{1/2}$) values were also the lowest under such aeration (Fig. 3(A)).

The control soils differed in the duration of the lag phase (Fig. 1), and therefore, the CH_4 uptake started at a different O_2 concentration (see Table 2) as a result of microbial respiration. In all control soils incubated under oxia (20% O_2), the CH_4 uptake started when the O_2 content ranged from ~ 18.3 to 19.2% *v*/*v*, and the O_2 concentration at the end of incubation did not drop below ~ 17% *v*/*v*. Under hypoxia, methanotrophy was initiated at the O_2 concentration ranging from 9.70 to 6.84% *v*/*v* (under 10% O_2) and from 4.47 to 2.72% *v*/*v* (under 5% O_2), and finally it did not decline below 5.5 and ~ 1% *v*/*v* O_2, respectively, on the day of the complete CH_4 uptake. Under microoxia conditions (2% O_2), slight CH_4 consumption started at the O_2 concentration ranging from ~ 0.4 to 1.44% *v*/*v*, and O_2 was completely consumed in this treatment at the end of incubation.

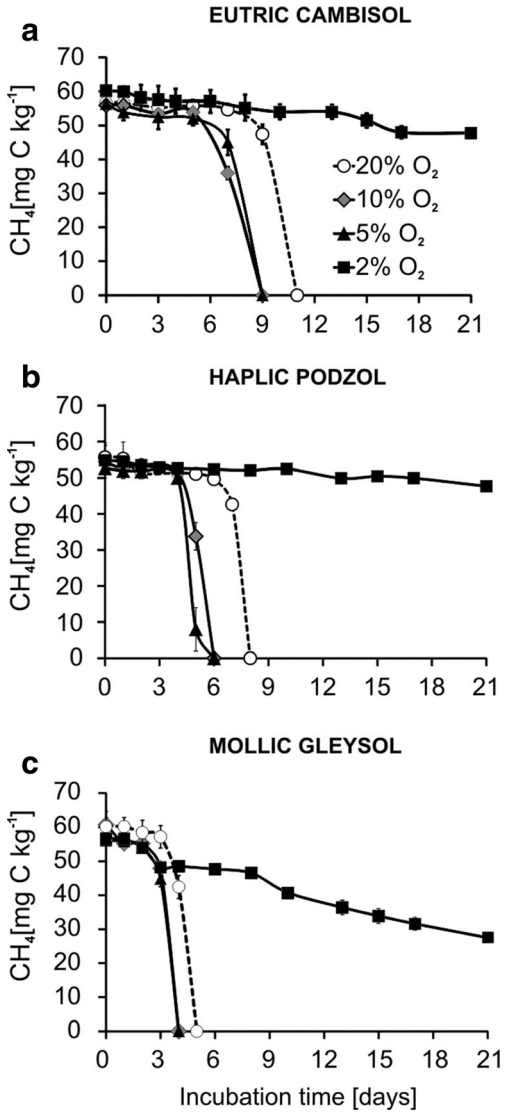

Fig. 1 Decrease in the CH_4 concentration with the time in the headspace of controls (without NH_4^+) of Eutric Cambisol, Haplic Podzol, and Mollic Gleysol (without NH_4^+) incubated with CH_4 (1% *v/v*). Soil samples were incubated under different O_2 levels (20%, 10%, 5%, 2% O_2 *v/v*). Points are averages of three replicates; bars indicate the standard deviations. 20% O_2—open circles; 10% O_2—gray rhombus; 5% O_2—black triangle; 2% O_2—black square

Methane oxidation in soils with ammonium and under different oxygen levels

The NH_4^+ addition changed the CH_4 uptake in all tested soils (Fig. 2) and influenced the duration of both phases depending on the O_2 level. Moreover, we observed different curve shapes of the induced phase. Generally, the CH_4 consumption started earlier in the ammonium-amended soils than that in the controls, but next the process slowed down or was even stopped.

In the Eutric Cambisol, strong inhibition by NH_4^+ was observed in all O_2 levels (Fig. 2(A)). Apparently, there was no (or a very slight) induction of the process at both 20 and 2% O_2. A short-term CH_4 consumption occurred at high (5% O_2) and low (10% O_2) hypoxia already after 1-day incubation. This means that, under moderate O_2 deficiency (hypoxia), CH_4 consumption in this ammonium-amended soil initiated much earlier than that in the control without NH_4^+ (see Fig. 2(A)). However, this stimulation was short-lived and finally only approx. 30% of the added CH_4 was consumed.

In the case of the Haplic Podzol (Fig. 2(B)), strong inhibition by NH_4^+ was observed under oxia (20% O_2), while hypoxia (5% O_2 and 10% O_2) resulted in the faster initiation of the CH_4 uptake. However, in contrast to the Eutric Cambisol, all added CH_4 was consumed under hypoxia in the ammonium-amended Haplic Podzol, although it lasted much longer than in the non-amended control (i.e., 14–16 days vs. 6 days). Microoxic conditions (2% O_2) strongly inhibited methanotrophy in the Haplic Podzol, like in the control.

After NH_4^+ addition to the Mollic Gleysol, the CH_4 uptake started almost immediately (on the first incubation day) at 20%, 10%, and 5% O_2 (Fig. 2(C)). In this soil, the highest

Table 2 Oxygen concentration at the beginning of CH_4 consumption in the headspace of the Eutric Cambisol, Haplic Podzol, and Mollic Gleysol soils incubated without (controls) or with ammonium (NH_4^+) under different O_2 levels (avg ± SD, $n = 3$)

	Tested soils	O_2 level	O_2 concentration [%, *v/v*]
Controls (without NH_4^+)	Eutric Cambisol	20% O_2	18.5 ± 0.16
		10% O_2	7.95 ± 0.18
		5% O_2	3.58 ± 0.21
		2% O_2	0.395 ± 0.01
	Haplic Podzol	20% O_2	18.32 ± 0.28
		10% O_2	6.84 ± 0.71
		5% O_2	2.72 ± 0.39
		2% O_2	0.408 ± 0.09
	Mollic Gleysol	20% O_2	19.20 ± 0.44
		10% O_2	9.70 ± 0.64
		5% O_2	4.47 ± 0.12
		2% O_2	1.44 ± 0.10
Soils with NH_4^+	Eutric Cambisol	20% O_2	19.99 ± 0.08
		10% O_2	10.00 ± 0.09
		5% O_2	5.01 ± 0.19
		2% O_2	1.03 ± 0.13
	Haplic Podzol	20% O_2	16.39 ± 0.40
		10% O_2	9.57 ± 0.20
		5% O_2	5.01 ± 0.17
		2% O_2	0.408 ± 0.04
	Mollic Gleysol	20% O_2	20.35 ± 0.28
		10% O_2	10.08 ± 0.54
		5% O_2	5.12 ± 0.25
		2% O_2	1.80 ± 0.14

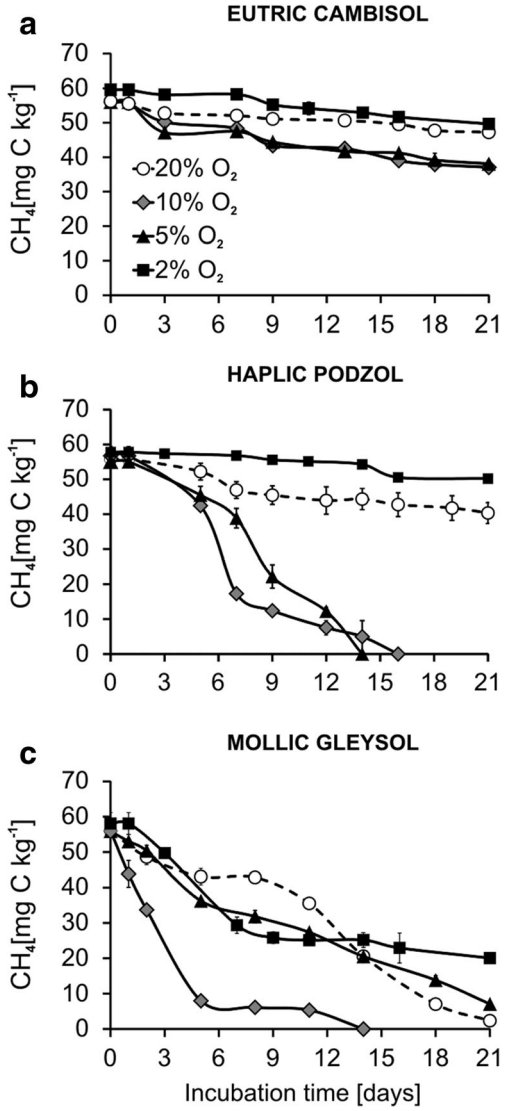

Fig. 2 Decrease in the CH_4 concentration with the time in the headspace of Eutric Cambisol, Haplic Podzol, and Mollic Gleysol incubated with CH_4 (1% *v*/*v*) and with NH_4^+ (100 mg N kg^{-1}) addition. Soil samples were incubated under different O_2 levels (20%, 10%, 5%, 2% O_2 *v*/*v*). Points are averages of three replicates; bars indicate the standard deviations. Open circles for 20% O_2; gray rhombus for 10% O_2; black triangle for 5% O_2; black square for 2% O_2

CH_4 oxidation rate was observed under low hypoxia (10% O_2) with complete CH_4 oxidation within 14 days. At higher O_2 availability, 10% and 20% O_2, 87% and 96% of added CH_4 was consumed, respectively. Under microoxia (2% O_2), the CH_4 uptake started in this soil after a short 1-day lag period and proceeded for 9 days; finally, 65% of the added CH_4 was consumed.

The CH_4 oxidation rates calculated for the ammonium-treated soils were lower and the $t_{1/2}$ values were much higher than for controls (Fig. 3(A, B)). However, under microoxia (2% O_2), as revealed by the analysis of variance, the NH_4^+ application increased the CH_4 oxidation rate in the Mollic Gleysol (by ca. 30%, $p < 0.05$). In all ammonium-amended soils, the highest methanotrophic activity was observed under hypoxia (5% or 10% O_2) ($p < 0.05$) with the rate values ranging from about 0.9 mg CH_4-C kg^{-1} day^{-1} (Eutric Cambisol) to about 4 mg CH_4-C kg^{-1} day^{-1} (Haplic Podzol and Mollic Gleysol). Therefore, the lowest half-life values were recorded under hypoxia in all tested soils (Fig. 3(B)).

The NH_4^+ addition to the tested soils reduced the duration of the lag phase (Fig. 2) in comparison to controls (Fig. 1). Therefore, methanotrophy was initiated at higher O_2 concentrations than in the controls (Table 2). In ammonium-amended soils incubated under oxia (20% O_2), the CH_4 uptake started when O_2 ranged from 20.3 to 19.5% *v*/*v*, and did not drop below 12.2% *v*/*v* O_2. Under hypoxia, CH_4 uptake started at once at the initial O_2 concentrations of 10% and ~ 5% *v*/*v* O_2 and did not decline below 4.8% and 2.8% under high and low hypoxia, respectively. Under microoxic conditions (2% O_2), the consumption started at the O_2 concentration ranging from 0.41 to 1.80% *v*/*v* O_2 (Table 2). As in the controls, oxygen was completely consumed at the end of incubation.

Discussion

Our experiment confirms the great importance of the soil oxygen level during the studies on CH_4 oxidation. We simulated field soil conditions and processes that occur in the soil agroecosystems. Our laboratory incubation experiment may be useful in understanding the environmental consequences of C and N interactions.

Oxygen effect on methane oxidation in soils

Oxygen is an electron acceptor for methane oxidation (He et al. 2011) and the major limiting factor in aerobic methanotrophy (Chowdhury and Dick 2013; Wilshusen et al. 2004). O_2 is needed in the first step of aerobic methane oxidation for the conversion of methane to methanol (He et al. 2011), and this reaction is catalyzed by methane monooxygenase (MMO) (Hanson and Hanson 1996). We have hypothesized that CH_4 consumption at the different oxygen levels may depend on the sensitivity of MMO to O_2; some methanotrophs may adapt to low oxygen conditions via specific metabolic strategies (Henckel et al. 2000; Hernandez et al. 2015; Kalyuzhnaya et al. 2013, Ward et al. 2004). Our experiment showed that the O_2 level differentiated the CH_4 consumption in three mineral soils. Probably, O_2 as a substrate for MMO should increase CH_4 oxidation as suggested by Chi et al. (2012) and Pawłowska et al. (2011). In our experiment, the methanotrophic activity did not decrease at the lower O_2 concentration. Generally, the tested soils (not amended with NH_4^+) oxidized all added CH_4 in the O_2 range from oxia (20% O_2) to high hypoxia (5% O_2) (Fig. 1). However, low (10% O_2) and high (5% O_2) hypoxia levels

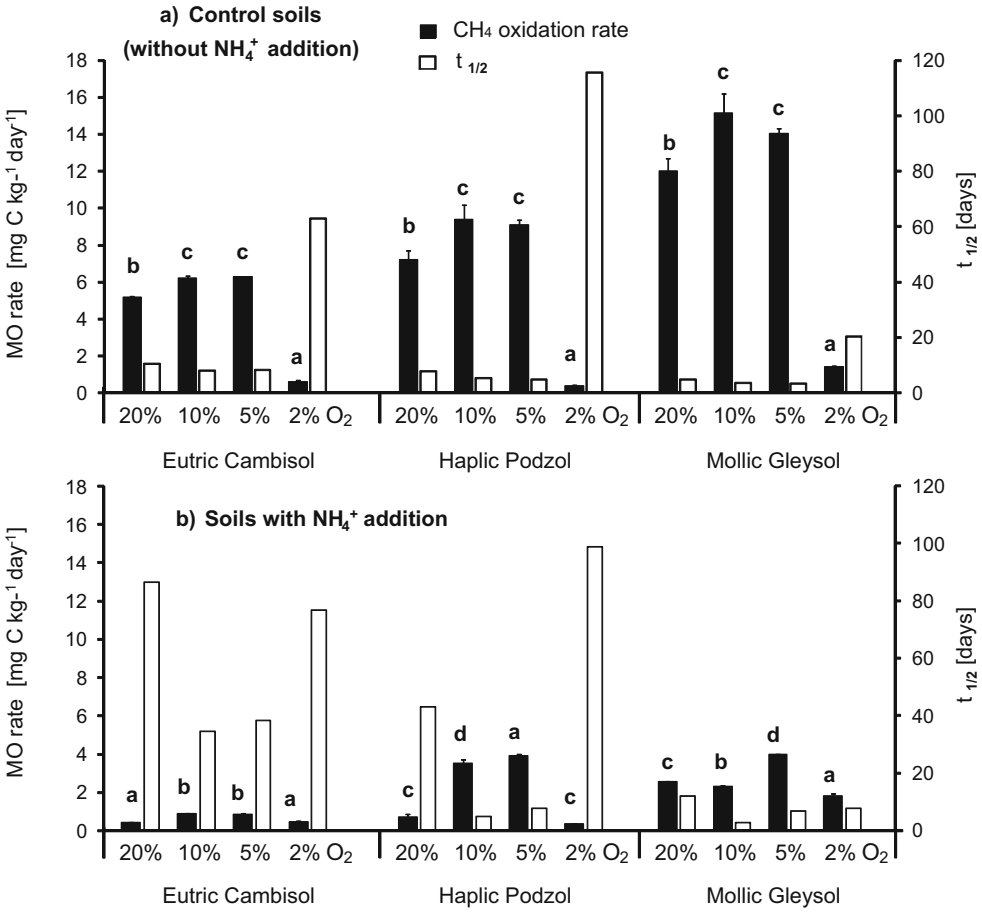

Fig. 3 Average CH_4 oxidation rates (avg ± SD, $n = 3$) and half-life value in Eutric Cambisol, Haplic Podzol, and Mollic Gleysol enriched with CH_4 (1% *v*/*v*) and without (control) or with NH_4^+ (100 mg N kg^{-1}). Soil samples were incubated under different O_2 levels (20%, 10%, 5%, 2% O_2 *v*/*v*). The same letters above the columns indicate no statistically significant differences among the rates (one-way ANOVA, Tukey post hoc test, $p < 0.05$, calculated separately for each soil)

were usually more favorable than oxia for methanotrophic activity (Fig. 3). Similarly, Wnuk et al. (2017) reported enhanced CH_4 oxidation rate in the same Eutric Cambisol, at higher than in lower moisture. Despite the tested soils samples were characterized by the same initial O_2 concentration and the same O_2 diffusion due to similar texture, they differed in the duration of the lag phase due to the specific soil properties. Therefore, the real O_2 concentrations varied at the beginning of CH_4 consumption (Table 2), which did not reach the values at the next O_2 level. Our results directly confirmed higher methanotrophic activity under low O_2 concentration, whose value depends on soil water content. Oxygen at the level ≤ 5% was reported by Duan et al. (2017) as critical O_2 concentration below which CH_4 oxidation (1%) was reduced in slurry surface crusts. Our microoxic conditions (2% O_2) inhibited or retarded CH_4 oxidation, likely due to the effect of the O_2 depletion during incubation. Such an O_2 concentration (Table 2) could be too low for methanotrophs inhabiting the tested soils due to its complete consumption during incubation. However, Wilshusen et al. (2004) showed slightly higher and more stable activity for leaf compost at 1.5% O_2 than 10.5% O_2. Czepiel et al. (1996) demonstrated that the methanotrophic activity in a landfill spoil layer decreased at an O_2 level below 3% O_2, but was not sensitive to higher O_2 concentrations.

Biphasic kinetics of CH_4 consumption was observed in the control soil samples (without NH_4^+ addition) incubated at O_2 in the range from 20 to 5% O_2. Such a curve shape was reported previously by Bender and Conrad (1992, 1995) and Steenbergh et al. (2010). The process was initially slow, but next, the rate increased in the induced phase. The proposed mechanisms explaining the nonlinear CH_4 consumption include (1) growth of methanotroph populations (Bender and Conrad 1992, 1995; Cai and Yan 1999; Henckel et al. 2000); (2) increased cell activity (Gilbert and Frenzel 1998; Henckel et al. 1999); (3) combinations of growth and increased cell activity (Steenbergh et al. 2010); (4) a low percentage participation of active methanotrophs in the lag phase (Steenbergh et al. 2010); and (5) changes in the specific activity of methanotrophs, the number of bacteria, and the CH_4 concentration (Cai and Yan 1999). The period of low CH_4 oxidation (lag phase) can last up to several days (Syamsul Arif et al. 1996) and in long-term fertilized soil even up to 2–3 weeks (Hütsch 2001). In our experiment, the initial phase was shorter under hypoxia than under oxic conditions, which may suggest that reduced O_2 availability in non-fertilized soil

creates better conditions for activity and growth of methanotrophs. The next phase of the rapid CH_4 depletion took the same time for both oxic and hypoxic conditions (2–4 days).

In our study, the CH_4 consumption rate ranked as Eutric Cambisol < Haplic Podzol < Mollic Gleysol, likely depending on the presence of different species of methanotrophic bacteria and for different properties of the used soils. The Mollic Gleysol was characterized by relatively high organic C content (C_{org} 3.93%, Table 1), which may have created better conditions for microbial activity, including that of methanotrophy. In this soil, the half-life values were lower than those in Cambisol and Podzol (even at 2% O_2; Fig. 3), which confirmed its high methanotrophic activity.

Ammonium effect on methane oxidation in soils under different O_2 levels

The O_2 status may have a direct impact on methanotrophic bacteria as well as it can act indirectly by affecting N transformation. Application of both mineral and organic N fertilizers may induce several processes, including denitrification and nitrification (Trimpler et al. 2016). Therefore, not only the O_2 level alone, but the combined effect of soil aeration and N (entering the soil through the high N fertilizers input) may have important environmental consequences. Interactions between O_2 and the availability of NH_4^+ can control the rate of nitrification (Caffrey et al. 2003). Since nitrification under reduced O_2 concentration has been observed (Goreau et al. 1980; Sliekers et al. 2005), we suppose that nitrifying bacteria, besides methanotrophs, may also consume CH_4 (Mohanty et al. 2016; Xu and Inubushi 2004) under hypoxia in our study. However, the intermediate products of NH_4^+ oxidation, e.g., hydroxylamine and nitrite (NO_2^-), can be toxic to methanotrophic bacteria and thus may inhibit CH_4 consumption (Alam and Jia 2012; Dunfield and Knowles 1995; Schnell and King 1994; Zheng et al. 2013).

In our experiment, after NH_4^+ application, the highest reduction of CH_4 oxidation in all soils was observed under oxia (20% O_2) (Figs. 2 and 3). Under 2% O_2 and with NH_4^+ application, the CH_4 oxidation rate and half-life value were only slightly changed in comparison to the soil samples without NH_4^+ addition, especially in the Cambisol and Podzol. Moreover, in the ammonium-amended Mollic Gleysol, about a half of CH_4 (32 mg CH_4-C kg^{-1}) was consumed until the eighth incubation day under microoxia, i.e., even more than in the control. In the ammonium-amended Eutric Cambisol, low CH_4 consumption occurred under hypoxia (5% and 10% O_2) and it was stopped after few days. The application of NH_4^+ to Haplic Podzol strongly delayed methanotrophic activity and CH_4 was completely oxidized only under hypoxia (5% and 10% O_2) (Fig. 2).

Interestingly, the NH_4^+ addition reduced the lag phase to 1 day under high (5% O_2) and low (10% O_2) hypoxia in Eutric Cambisol and Haplic Podzol and in the next day inhibition or slowdown (respectively) occurred (Fig. 2). In the ammonium-amended Mollic Gleysol, the process began immediately except for microoxia, and this resulted in the lowest half-life values. However, the average CH_4 oxidation rate was significantly lower than that in the soil without NH_4^+ (Fig. 3), probably due to accumulation of NO_2^- and/or other nitrification intermediates. We hypothesize that the NH_4^+ addition relieved N limitation initially and reduced the lag phase. Bodelier et al. (2000) also showed the initiation of CH_4 oxidation without a delay phase in an ammonium-amended rice field soil probably due to the use of NH_4^+ as a N source. The rate of CH_4 oxidation is usually constant over time (Steenbergh et al. 2010). However, in the ammonium-amended soils, we observed periods with a higher and lower rates, especially in more active Mollic Gleysol, probably due to the interference of nitrification products. In the ammonium-amended Mollic Gleysol and Haplic Podzol, methane oxidation rates were even higher under 5% O_2 than under 10% O_2 ($p < 0.05$), contrarily to the controls showing slightly higher rates under 10% O_2 than under 5% O_2 (Fig. 3).

Other mechanisms have been proposed to explain the effects of N forms on CH_4 oxidation in soil. High concentration of NH_4^+ salt can affect the CH_4 oxidation by the nonspecific effect of the salt (osmotic stress) (Rigler and Zechmeister-Boltenstern 1999; Saari et al. 2004; Whalen 2000). Competitive inhibition by NH_4^+ ions is a mechanism often proposed in different soils (Alam and Jia 2012; Bender and Conrad 1995; Bronson and Mosier 1994; Dunfield and Knowles 1995; Schnell and King 1994; Zheng et al. 2013). Both methanotrophs and nitrifiers have several enzymes in common, in particular ammonia monooxygenase vs. particulate methane monooxygenase (MMO). A short-term decline in methanotrophic activity can be due to the competitive inhibition of MMO by NH_4^+ due to structural similarity of ammonium and methane molecules. Even though the affinity of MMO for methane is 600–1300-fold higher than that for NH_4^+, high concentrations of NH_4^+ can inhibit methanotrophic activity (Bèdard and Knowles 1989). The different responses of soils in our study to NH_4^+ under a different O_2 status can be due to dominance of different species of methanotrophic bacteria (which should be confirmed by microbial analyses).

However, the addition of NH_4^+ can also stimulate methanotrophic activity by changing the C:N ratio (Rigler and Zechmeister-Boltenstern 1999). Methanotrophic bacteria have a relatively high N demand for growth and protein synthesis, as for each mole of assimilated CH_4-C, they need 0.25 mol of N (Anthony 1982). Indeed, the size and activity of a methanotrophic population in a rice rhizosphere

increased after the addition of urea or $(NH_4)_2PO_4$ (Bodelier et al. 2000). Stimulation of CH_4 uptake on fertilized paddy fields was observed under both field and laboratory conditions (Dan et al. 2001; Krüger and Frenzel 2003), whereas He et al. (2011) reported that the process in landfill cover soil was higher under an ambient O_2 concentration than under 3% O_2. Our results showed the environmental effects of different O_2 levels and N fertilization on methane oxidation. Mineral N form content and O_2 level are not constant in soil and their changes can affect soil microbial activity. The tested soils were characterized by similar particle size distribution and, hence, similar air-water conditions; however, they differed in the organic C content (Table 1). Considering soil type, it should be pointed that sandy loam soil (Cambisol) inhibited CH_4 consumption in the presence of NH_4^+, whereas the opposite occurred in the loamy sand (Gleysol). The multi-factor analysis of variance showed that, generally, the methanotrophic activity was significantly influenced by the factors in the following order: NH_4^+ concentration ($p = 0.000$, $F = 28.97$) > O_2 level ($p = 0.008$, $F = 4.15$) > soil properties ($p = 0.031$, $F = 3.58$).

In conclusion, our experiment showed that the methanotrophic activity ranked as Eutric Cambisol < Haplic Podzol < Mollic Gleysol. However, all soil samples without NH_4^+ addition completely oxidized the added CH_4 under oxia (20% O_2) to high hypoxia (5% O_2) and high reduction of the process occurred under microoxia (2% O_2). Hypoxia was usually more favorable than oxia for CH_4 oxidation. The addition of NH_4^+ reduced the lag period, with a decrease or even inhibition of CH_4 oxidation, which can be explained by (1) competitive inhibition and (2) an effect of the intermediate products (such as NO_2^-) of nitrification. Under high hypoxia (5% O_2), the negative influence of NH_4^+ on methanotrophic activity decreased. The methane oxidation rate was significantly ($p < 0.001$) affected by NH_4^+ and O_2 in all the tested soils; however, the NH_4^+ effect was stronger than that of O_2. The reported contrasting results of NH_4^+ on soil CH_4 oxidation may be partly explained by the O_2 level. Further studies should focus on methanotrophy in other soil types under different O_2 levels. Moreover, both microbial tests and determination of the activity of isolated MMO under different O_2 concentrations would be useful for better understanding the mechanisms underlying our results.

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