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Nicolas Bras, Caroline Plain, Daniel Epron. Potential soil methane oxidation in naturally regenerated oak-dominated temperate deciduous forest stands responds to soil water status regardless of their age-an intact core incubation study. *Annals of Forest Science*, 2022, 79, pp.29. 10.1186/s13595-022-01145-9 . hal-03858826

HAL Id: hal-03858826

<https://hal.univ-lorraine.fr/hal-03858826>

Submitted on 17 Nov 2022

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RESEARCH PAPER

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Potential soil methane oxidation in naturally regenerated oak-dominated temperate deciduous forest stands responds to soil water status regardless of their age—an intact core incubation study

Nicolas Bras¹, Caroline Plain^{1*}  and Daniel Epron^{1,2} 

Abstract

Key message: Potential CH₄ oxidation in the top soil layer increased with decreasing soil water content in spring but was inhibited during severe summer drought in naturally-regenerated oak-dominated temperate deciduous forest stands regardless of their age. No direct effect of mineral nitrogen on soil CH₄ oxidation was found. Soil CH₄ oxidation in temperate forests could be reduced by extreme climatic events.

Context: The oxidation of atmospheric methane (CH₄) by methanotrophic bacteria in forest soils is an important but overlooked ecosystem service.

Aim: Our objective was to determine which factors drive variations in soil CH₄ oxidation in oak-dominated temperate deciduous forest stands of different ages.

Methods: Soil samples were collected in 16 stands aged 20 to 143 years in periods of high and low soil water content (SWC). The potential rate of soil CH₄ oxidation was measured by incubating the first five centimetres of intact soil cores at 20 °C.

Results: SWC was the main driver accounting for variations in CH₄ oxidation. In spring, a two-fold reduction in SWC greatly increased CH₄ oxidation. But when the soil was dry in late summer, a further reduction in SWC led to a decrease in CH₄ oxidation in the top soil layer. No direct effect of mineral nitrogen on soil CH₄ oxidation was found.

Conclusions: With regard to soil CH₄ oxidation, naturally regenerated forest stands contribute equally to climate change mitigation regardless of their age. Considering future climate scenarios for Europe, soil CH₄ sink in temperate forests could be reduced, due to both an increase in the number of flooding episodes in spring and drier summers.

Keywords: Methane oxidation, Naturally regenerated forest, Air-filled porosity, Mineral nitrogen, Water stress, Chronosequence

Handling Editor: Alexia Stokes

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1 Introduction

The atmospheric concentration of methane (CH₄), which is the second most important greenhouse gas contributing to global warming, has increased from 0.75 ppmv to 1.85 ppmv in the past 200 years (Saunois et al. 2020; IPCC 2021). The main CH₄ sinks are dependent on



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oxidation with hydroxyl radicals in the troposphere and biological oxidation in the soil by CH₄-oxidising bacteria (Wuebbles 2002). Among the different types of land uses, forest soils show the greatest CH₄ oxidation rate at 4.2 kg CH₄ ha⁻¹ year⁻¹ while the oxidation rate of other types of soils is about 1.6 kg CH₄ ha⁻¹ year⁻¹ (Dutaur and Verchot 2007).

One of the factors that has the greatest impact on CH₄ oxidation is the soil's air-filled porosity, in other words, the open space between soil particles that is filled with air (Epron et al. 2016; Fest et al. 2017). The air-filled porosity depends on both bulk density (BD) and volumetric soil water content (SWC). The diffusion of gases, including CH₄ and dioxygen (O₂), from the atmosphere into the soil increases with decreasing SWC (Smith et al. 2003), which stimulates CH₄ oxidation. On the other hand, high SWC, resulting in low diffusion of gases into the soil, leads to lower methanotrophic activity and can even cause anaerobic conditions that favour the production of CH₄ by methanogenic archaea (Veldkamp et al. 2013). A seasonal variation in CH₄ oxidation has been observed in several European forests, with higher oxidation in summer and early fall when soils are drier than in winter and earlier spring when SWC is high (Guckland et al. 2009; Epron et al. 2016).

Mineral nitrogen (N) affects CH₄ oxidation, either inhibiting or stimulating it depending on the form of the nitrogen and its concentrations, and on the methanotroph community (Carlsen et al. 1991; Hütsch 1998; Saari et al. 2004; Bodelier and Laanbroek 2004; Alam and Jia 2012). Some methanotrophic bacteria switch to ammonia oxidation when ammonia concentrations in the soil are high because ammonia acts as a competitive inhibitor of CH₄ monooxygenases (O'Neill and Wilkinson 1977). Nitrite and nitrate can also inhibit CH₄ oxidation by methanotrophic bacteria (Seghers et al. 2003; Mochizuki et al. 2012). However, mineral N can also stimulate methanotroph activity when nitrogen is a limiting factor for microbial growth (Bodelier and Laanbroek 2004). In forests, the rate of CH₄ oxidation was found to increase with the amount of available nitrogen (Goldman et al. 1995) and when low amounts of nitrogen fertilisers were added (Rigler and Zechmeister-Boltenstern 1999; Veldkamp et al. 2013; Martinson et al. 2021).

Mineral N and SWC vary seasonally and can also change over time with the aging of forest stands. Indeed, mineral N is thought to increase with stand age due to cumulative atmospheric N deposition, increased N mineralisation and the decreased N requirements of trees (Hansen et al. 2007; Christiansen and Gundersen 2011; Rahman et al. 2017). Higher porosity in older stands compared to young stands at least partly explained higher CH₄ oxidation in some previous studies (Peichl et al.

2010; Christiansen and Gundersen 2011; Bárcena et al. 2014; Zeng et al. 2014). An increase in soil organic matter over time after afforestation usually results in an increase in soil porosity (Boivin et al. 2009). Moreover, decomposition resulting from root growth may also increase soil porosity (Bodner et al. 2014). Older stands may also have higher evapotranspiration, which would result in lower SWC, therefore improving gas diffusion (Farley et al. 2005; Hiltbrunner et al. 2012). However, it is not certain that SWC decreases as forest stands age because lower evapotranspiration in older stands than in young stands may be due to lower tree densities resulting in a lower leaf area index. Furthermore, greater tree height may result in lower stomatal conductance (Alsheimer et al. 1998; Delzon and Loustau 2005). A few studies have found an increase in CH₄ uptake measured in situ with the aging of forest stands linked to a decrease in SWC while others did not find any effect of stand age on CH₄ oxidation related to SWC (Peichl et al. 2010; Christiansen and Gundersen 2011; Hiltbrunner et al. 2012; Fest et al. 2015). However, most previous studies on the effect of stand age on CH₄ oxidation were conducted on afforested chronosequence established on abandoned agricultural lands, not on naturally regenerated forest stands.

Our objective in this study was to determine the influence of soil bulk density, water content and mineral N on spatial and temporal variations in soil CH₄ oxidation in a 470-ha oak-dominated temperate deciduous forest. We measured the potential rate of CH₄ oxidation in the top soil layer, SWC, BD and mineral N concentrations on intact soil cores collected in 16 neighbouring stands of sessile oak, aged 20 to 143 years. We hypothesised that (1) variations in CH₄ oxidation would be related to differences within and among-stand in SWC, BD and mineral N content, as well as their seasonal variations and (2) CH₄ oxidation would increase with stand age, reflecting changes in SWC, BD and mineral N content over time.

2 Materials and methods

2.1 Description of the site and the stands

The study was conducted in the state forest of Champenoux (48°43' N, 6°21' E, mean elevation 260 m, 470 ha) in the northeast of France. The soils are neoluvisols on a carbonated clay horizon covered by rather deep loam (Bréda et al. 1993). The climate is semi-continental. Annual mean temperature for the past 30 years is 11 °C and annual average precipitation 808 mm based on data from the nearest weather station (Essey-les-Nancy, 12 km, Météo-France 2020).

Sixteen forest stands dominated by sessile oak (*Quercus petraea* (Matt.) Liebl.) were selected (Table 1). Thirteen of these stands, previously included in a chronosequence study (Genet et al. 2010), were between 40 and 143 years

Table 1 Characteristics of the 16 selected stands in an oak-dominated naturally regenerated forest

Stand ID	Age (year)	Basal area (m ² ha ⁻¹)	Density (trees ha ⁻¹)	Sampling campaign
1	20	12.2	19367	3
2	26	20.4	7167	3
3	26	29.2	11875	3
4	40	25.7	2742	1, 2, 3
5	50	35.2	2033	1, 2, 3
6	50	27.5	3917	1, 2, 3
7	60	27.9	2392	1, 2, 3
8	60	35.6	2925	1, 2, 3
9	86	29.4	858	1, 2
10	89	31.1	892	1, 2
11	89	43.7	1058	1, 2
12	128	27.5	858	1, 2
13	129	23.5	608	1, 2
14	129	25.2	942	1, 2
15	139	24.5	550	1, 2
16	143	26.4	933	1, 2

The numerical digits in the last column refer to the sampling campaigns where the stand was included: 1 September 17–October 9, 2018, 2 March 25–April 13, 2019, 3 August 27–September 5, 2019

old; they were studied in fall 2018 and spring 2019. In summer 2019, five of the previous stands were resampled (age 40–60 years) and three younger stands (20 to 26 years old) were added to ensure that the absence of age effect on CH₄ oxidation observed in older stands (see the Section 3), was also verified for younger stands. Special care was taken to minimise variations in soil type and topography. All the stands were even-aged and naturally regenerated. In each stand, a 1200-m² plot was established and the girth at breast height of all the trees in the plot with a girth of more than 10 cm was measured to calculate stand basal area.

2.2 Soil sampling

Soil samples were collected during three campaigns: in early fall 2018 (September 17–October 9) and late summer 2019 (August 27–September 5) during periods of low SWC; and in early spring 2019 (March 25–April 13) during a period of high SWC. In fall 2018 and spring 2019, samples were collected in the oldest 13 of the 16 stands while in summer 2019 samples were collected in the eight youngest stands. Five stands were therefore sampled during the three sampling campaigns.

In each 1200-m² plot, a 30 × 40 m-grid was installed, then subdivided into 12 squares (10 × 10 m). After removal of the fresh litter, metal cylinders (8 cm in diameter) were used to take soil samples (0–5 cm deep) within each square. Two or three samples in each stand were

collected every two or three days over a 14-day period so that sampling day would not be a confounding factor for the stand.

2.3 Potential rates of CH₄ oxidation and CO₂ production in the top soil layer

Twelve cylinders each containing a soil sample were mounted with two plastic lids, leaving a headspace over the soil sample which, together with the tubing and the analyser cell, occupied a volume of 0.84 L. The 12 cylinders were connected to an off-axis integrated cavity output spectroscopy gas analyser (GGA-24EP, Los Gatos Research, Mountain View, CA, USA) that measured the methane, carbon dioxide and water vapour concentrations in the headspace atmosphere. The incubation of the intact cores was done in a climatic chamber (Memmert, IPP260) where the temperature was kept at 20 °C during the measurements. The gas concentrations in the cylinder headspace were measured for 1 to 2 h, recorded every 5 s and stored on a datalogger (CR1000, Campbell Scientific Inc., Logan, UT, USA). After the measurement of one cylinder was completed, the system was purged and two gases with known concentrations of CH₄ (5 and 0 ppm) and CO₂ (600 and 0 ppm) were flushed through the analyser for 2 min to calibrate the system before measuring the next cylinder. Solenoid valves (LVM10R1-6B-1-Q, SMC, Tokyo, Japan) controlled with relay controllers (SDM-CD16AC, Campbell Scientific Inc.) connected to the data-logger were used to switch measurements from one cylinder to the next.

Potential rates of CH₄ oxidation (in nmol m⁻² s⁻¹) and CO₂ production (in μmol m⁻² s⁻¹) were calculated from the slopes of the variations in concentrations over time, after discarding the first 360 s required to fully equilibrate the system. For CO₂, the slope of a linear function was calculated based on the next 240 s of measurements. We preferred a linear function for CO₂ over a short time period because CO₂ diffusion became limited when the concentrations in the cylinder headspace increased. For CH₄, the initial slope was determined by fitting an exponential function on all the remaining data. We chose an exponential function for CH₄ because oxidation was expected to decrease along with CH₄ concentration in the cylinder headspace due to CH₄ limitation.

2.4 Soil mineral nitrogen, water content, and bulk density

The weight of the cylinder with the soil core inside was measured before and after the incubation, and the fresh weight of the soil core was calculated as the difference in mass between the full cylinder and the empty cylinder. After incubation, the samples were sieved through a 2-mm mesh and stored at 4 °C before further analyses. Soil mineral N concentrations were measured on a 20-g

subsample of sieved soil. The soil was suspended in 0.1 L of potassium chloride solution (1 M), agitated for one hour in a rotary shaker and filtered through Whatman filter papers. The filtrate was stored at 4 °C for 2 weeks at the most before being analysed with a spectrometric continuous flow analyser (San⁺⁺, Skalar, 4823 AA Breda, The Netherlands). Two different wavelengths (540 and 660 nm) were used to measure respectively ammonium (NH_4^+) and nitrite (NO_2^-) + nitrate (NO_3^-) nitrogen mass concentrations in the solution. Total mineral N was calculated as the sum of NH_4^+ and $\text{NO}_2^- + \text{NO}_3^-$.

To calculate SWC and BD, a 20-g subsample of the fine soil fraction was oven-dried at 105 °C for 24 h immediately following sieving, weighed and used to estimate the dry mass of the soil cores, knowing their total fresh mass and the subsample gravimetric water content.

In summer 2019 only, N mineralisation and net nitrification were measured by incubating at 20 °C the remaining sieved soil for 6 weeks during which SWC was kept constant. NH_4^+ and $\text{NO}_2^- + \text{NO}_3^-$ concentrations at the end of the incubation period were measured as described above. Net N mineralisation was calculated as the difference between the final mineral N content at the end of the incubation period and the initial mineral N content at the beginning of the incubation period divided by the incubation time. Net nitrification was calculated likewise using $\text{NO}_2^- + \text{NO}_3^-$ nitrogen mass instead of mineral N.

2.5 Statistics

Statistical analyses were performed with the R statistical software version 3.6.1 (R Core Team 2019). We performed one-way ANOVA to test the influence of forest stand on CH_4 oxidation, SWC, BD, soil mineral nitrogen and CO_2 production in fall 2018, spring 2019 and summer 2019, with 12 replicates per stands. We used linear mixed-effect models ('lmerTest' package, Kuznetsova et al. 2017), with stands as random effect, to estimate the effect of the season (fixed effect) on the same variables than above, using data of 13 stands (stand ID 4-16) to compare fall 2018 and spring 2019, and data of five stands (stand ID 4-8) to compare the three sampling dates. In the latter case, contrasts were used to test for seasonal differences when the overall model was significant ($p < 0.05$).

At the stand scale, we used non-linear models to study the relationship between stand age and either tree density or stand basal area. We used linear models to test the influence of stand age and stand basal area on CH_4 oxidation, SWC, mineral N concentration, CO_2 production, and BD separately for each sampling dates. We tested the combination of the two factors with or without interaction, and each factor independently, and selected the model for which all effects were significant. If more than one model would have met this requirement, we would

have selected the one with the lowest Akaike's Information Criterion (AIC). Linear regressions between CH_4 oxidation and the other variables were tested for each sampling date and are shown when the model was significant ($p < 0.05$). We fitted an exponential function on the relationship between SWC and nitrification.

At the sample scale, we used structural equation models (SEM) to analyse causal pathways through which soil water content and soil mineral nitrogen have direct effects on CH_4 oxidation and CO_2 production, and the covariation of these two processes at each sampling campaign. The initial model also included soil bulk density, but it was not included in the final model due to the lack of significant standardised path coefficients at all dates. SEM analyses were conducted using the R package "Lavaan" (Rosseel 2012). Models were retained if the χ^2 values of the fits were not significantly different from 0 ($p > 0.05$), the comparative fit index (cfi) were close to 1, and the root mean square error of approximation (rmsea) and the standardised root mean square residual (srmr) were both close to 0 (Kline 2016).

3 Results

Stand density decreased sharply with increasing stand age, especially in young stands up to 60 years of age, from 19,367 trees ha^{-1} to 550 trees ha^{-1} (Table 1, Fig. 1A). Stand basal area (BA) increased with stand age in young stands, from 12.2 $\text{m}^2 \text{ha}^{-1}$ to a maximum of 43.7 $\text{m}^2 \text{ha}^{-1}$ and tended to decrease with age in older stands (Table 1, Fig. 1B). Stand 11 exhibited noticeable high BA.

Potential CH_4 oxidation, SWC, mineral N concentrations, and CO_2 production in the top soil layer differed significantly from season to season while BD did not (Fig. 2). Higher CH_4 oxidation and lower SWC were measured in fall 2018 (respectively 0.66 $\text{nmol m}^{-2} \text{s}^{-1}$ and 0.17 $\text{m}^3 \text{m}^{-3}$ on average) than in spring 2019 (respectively 0.41 $\text{nmol m}^{-2} \text{s}^{-1}$ and 0.36 $\text{m}^3 \text{m}^{-3}$ on average; $p < 0.001$ for both differences) for the 13 stands aged from 40 to 143 years. When considering the five stands that were sampled at the three dates (aged from 40 to 60 years), the potential CH_4 oxidation in the top soil layer was lower in summer 2019 than in fall 2018 (respectively 0.42 $\text{nmol m}^{-2} \text{s}^{-1}$ and 0.60 $\text{nmol m}^{-2} \text{s}^{-1}$ on average, $p < 0.001$), while SWC was lower in summer 2019 than in fall 2018 (respectively 0.14 $\text{m}^3 \text{m}^{-3}$ and 0.17 $\text{m}^3 \text{m}^{-3}$ on average, $p < 0.001$). For the 13 stands 40 to 143 years old, mineral N was higher in spring 2019 (21 mg N kg^{-1} of dry soil) than in fall 2018 (12 mg N kg^{-1} of dry soil). However, in the five stands aged from 40 to 60 years, no significant differences in mineral N content were observed between fall 2018 and summer 2019. Ammonium represented on average 89% of the mineral N in our soils (data not shown). CO_2 production was higher in spring 2019 than

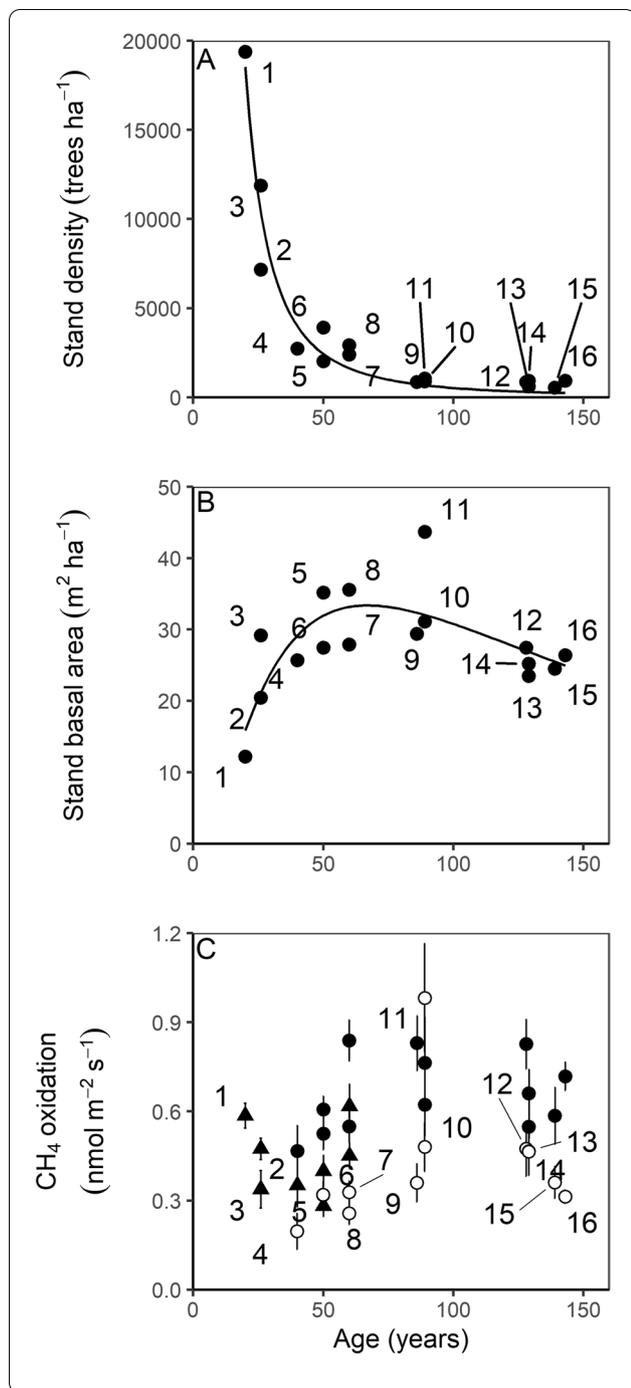


Fig. 1 Relationship between stand age and **A** stand density, **B** stand basal area, or **C** potential CH₄ oxidation in the top soil layer (intact soil cores) in fall 2018 (close circles), spring 2019 (open circles) and summer 2019 (close triangles) in 16 neighbouring stands of sessile oak, aged 20 to 143 years. In panel **A** and **B**, the solid lines show the fitted non-linear models: a power function for the relation between stand density and age ($R^2 = 0.95, p < 0.001$), and a three-parameter lognormal function for the relation between stand basal area and age ($R^2 = 0.56, p < 0.001$). There was no significant trend between CH₄ oxidation and age, regardless of season. Numbers are the ID of the stands, from youngest to oldest (shown only once in **C**, in summer 2019 for the three additional youngest stands added late and in fall 2018 for the 13 older stands)

in fall 2018 (respectively 8.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 2.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on average in 13 stands, $p < 0.001$), and lower in summer 2019 than in fall 2018 (respectively 0.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 3.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on average in 5 stands, $p < 0.001$).

Bulk density varied among stands from 0.8 kg dm^{-3} to 1.05 kg dm^{-3} , but with no trend related to stand age or stand basal area (data not shown). A significant effect of stand on potential CH₄ oxidation and SWC was

observed at the three sampling dates (Table 2). In spring 2019, average stand CH₄ oxidation in the top soil layer ranged from 0.20 to 0.98 $\text{nmol m}^{-2} \text{s}^{-1}$ and was positively related to both stand age and basal area (Table 3) but not to stand age alone (Fig. 1C). A similar trend, yet not significant ($p < 0.1$) was also observed in fall 2018, with a range of average CH₄ oxidation in the top soil layer between 0.47 and 0.84 $\text{nmol m}^{-2} \text{s}^{-1}$, but not in the dry summer 2019 (range 0.28 to 0.62 $\text{nmol m}^{-2} \text{s}^{-1}$). SWC was negatively related to stand basal area at all dates, although it was only a trend ($p < 0.1$) in fall 2018 and summer 2019 (Table 3). Therefore, a significant negative relationship between mean CH₄ oxidation and SWC in the top soil layer was observed in spring (Fig. 3A, $R^2 = 0.82, p < 0.001$). It should be noticed that the relationship was strongly influenced by stand 11, which exhibited high rates of CH₄ oxidation and low SWC, probably related to its high stand basal area mentioned above. Nevertheless, the relationship remained significant even with the removal of stand 11 ($R^2 = 0.49, p = 0.011$, not shown).

Soil mineral N differed among stands in fall 2018 and summer 2019, but not in spring (Table 2), with noticeable high concentration in stand 11 in fall 2018 and stand 5 in summer 2019. Soil mineral N was positively related to both stand age and basal area in fall 2018 (Table 3) but not at the other seasons. Between-stand variations in potential CH₄ oxidation in the top soil layer was significantly related to soil mineral N in summer 2019 (Fig. 3B, $R^2 = 0.55, p = 0.036$). However, the negative relation was strongly influenced by stand 5 and it should be noticed that if we remove stand 5, the relation is no longer significant. The net nitrification decreased exponentially with SWC in summer 2019 while no SWC effect was observed for the mineralisation of N (Fig. 4).

Soil CO₂ production, used in this study as a proxy for microbial activity in the top soil layer, differed among stands at the three sampling dates (Table 2), and was negatively related to the stand basal area at all dates, although it was only a trend ($p < 0.1$) in fall 2018

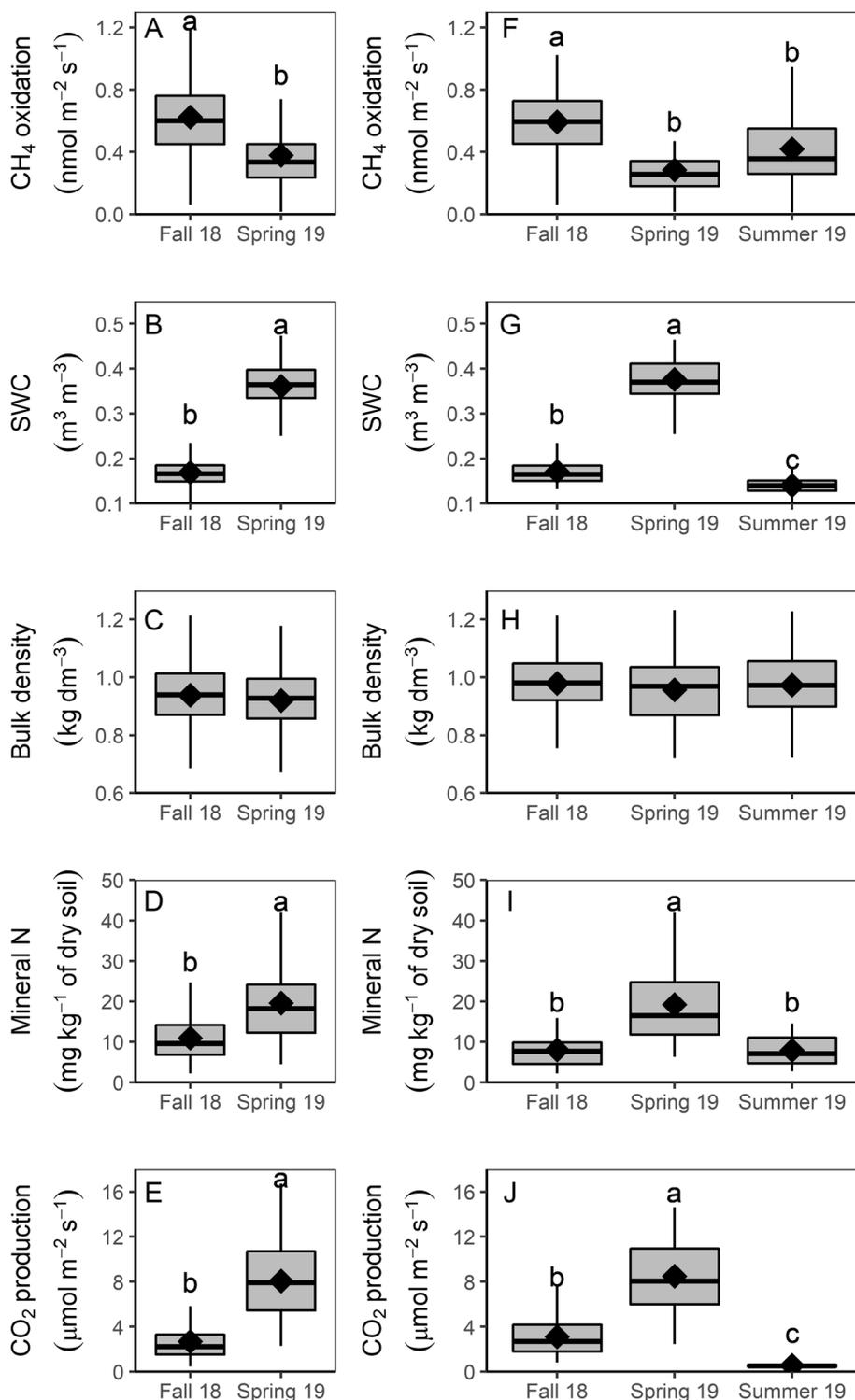


Fig. 2 Potential CH₄ oxidation (A, F), soil water content (SWC, B, G), bulk density (C, H), mineral nitrogen (D, I) and CO₂ production (E, J) of intact soil cores (0–5 cm in depth) incubated at 20°C. The box plots include values of 12 samples in 13 stands (*n* = 156) in fall 2018 and spring 2019 (left part of the figure: A–E) and values of 12 samples in five stands (*n* = 60) for the three sampling dates (right part of the figure: F–J). The horizontal thick line is the median; the diamond, the mean; the box, the interquartile range; the whisker, from the largest value no further than 1.5 times the upper quartile to the smallest value at most 1.5 times the lower quartile. Outliers (1 to 3 values) are not plotted to not extend the y-axis scale. Different letters indicate significant differences at *p* = 0.05 between seasons

Table 2 Influence of forest stand on potential CH₄ oxidation, soil water content (SWC), bulk density (BD), soil mineral nitrogen and CO₂ production of intact soil cores (0–5 cm in depth) at the three sampling periods

	Fall 2018	Spring 2019	Summer 2019
CH ₄ oxidation	0.01	< 0.001	< 0.001
SWC	< 0.001	< 0.001	< 0.001
BD	< 0.001	< 0.001	0.06
Mineral nitrogen	< 0.001	0.651	< 0.001
CO ₂ production	0.004	0.029	< 0.001
Degree of freedom	[12, 143]	[12, 143]	[7, 88]

Measurements were done on 13 stands in fall 2018 and spring 2019 (stand ID 4–16) and on 8 stands in summer 2019 (stand ID 1–8), with 12 replicates per stands. Degrees of freedom of the factor (stand ID) and of the residuals are given in the last row

Table 3 Results of linear models testing the effect of stand age and stand basal area, together (additive model) or separately, on mean values of potential CH₄ oxidation, soil water content (SWC), mineral N concentration and CO₂ production of intact soil cores (0–5 cm in depth) at the three sampling periods

Variable	Season	Explanatory		R ²	p value	df
		Age	BA			
CH ₄ oxidation	Fall 18	+	+	0.33	0.056	10
	Spring 19	+	+	0.56	0.006	10
	Summer 19	No model fits				
SWC	Fall 18		–	0.21	0.066	11
	Spring 19		–	0.34	0.036	11
	Summer 19		–	0.46	0.064	6
Mineral nitrogen	Fall 18	+	+	0.46	0.018	10
	Spring 19	No model fits				
	Summer 19	No model fits				
CO ₂ production	Fall 18	–	–	0.32	0.060	10
	Spring 19		–	0.56	0.002	11
	Summer 19		–	0.42	0.049	6

ANOVA p values and adjusted R² of the best models are presented. The direction of the effects of each factor are indicated (+ increasing; – decreasing). Bulk density was not included in the table because no model fitted the data at any of the dates

(Table 3). Between-stand variations in CH₄ oxidation was positively related to CO₂ production in summer 2019 (Fig. 3C, respectively R² = 0.68, p = 0.012).

Structural equation model (SEM) analysis conducted at the sample scale (156 soil cores in fall 2018 and spring 2019, and 96 cores in summer 2019) revealed a direct positive effect of SWC on CO₂ production at all sampling dates while the direct effect of SWC on potential CH₄ oxidation differed between the three sampling dates: not significant in fall 2018, negative in spring 2019, and positive in summer 2019 (Fig. 5). The significant covariation between CH₄ oxidation and CO₂ production in the top soil layer in summer 2019 confirmed the positive relationship found at stand level mentioned above (Fig. 3C).

The direct effect of SWC on soil mineral nitrogen was positive in fall 2018 and spring 2019, but negative in summer 2019. Soil mineral nitrogen had a direct effect on CO₂ production in spring 2019 only and had no effect on CH₄ oxidation at any sampling date. This suggests that the negative relationship between CH₄ oxidation and mineral N in the top soil layer at stand level mentioned above (Fig. 3B) was indirect, possibly mediated by soil water content.

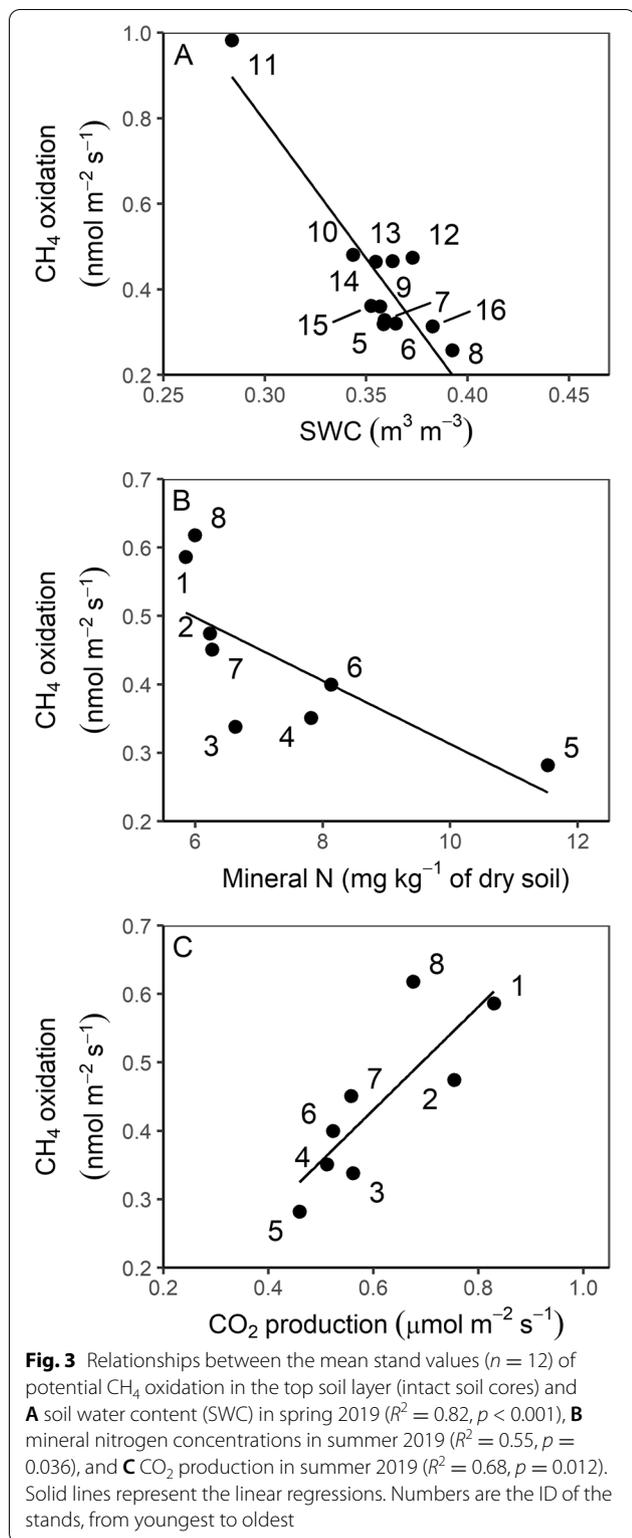
4 Discussion

4.1 Variations in methane oxidation were related to variations in soil water content

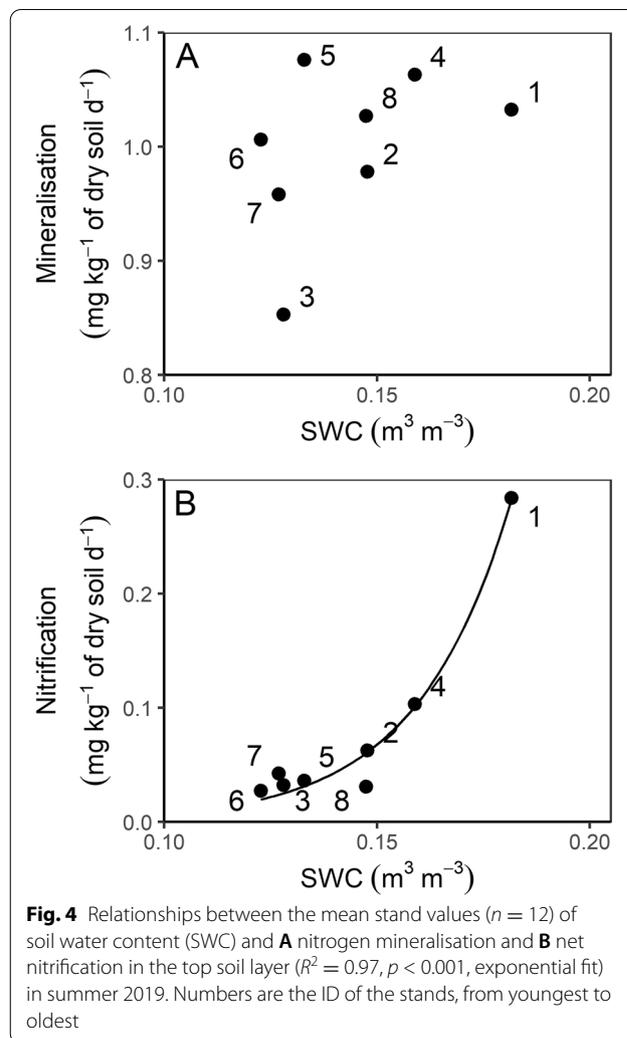
In agreement with our hypothesis (1), the potential CH₄ oxidation measured at 20 °C on intact soil cores was higher in late summer and early fall than in early spring

for all stands due to low SWC, which favoured gas diffusion, confirming the relationships observed between net surface fluxes measured in situ and SWC (Smith et al. 2003; Guckland et al. 2009; Epron et al. 2016). The fact that among-stand variations in CH₄ oxidation were negatively related to variations in SWC only in early spring suggests that gas diffusion was no longer a limiting factor for CH₄ oxidation in the top soil layer in late summer and early fall. The highest rate of CH₄ oxidation in spring was observed in stand 11, which also had the lower SWC.

The potential CH₄ oxidation in the top soil layer was higher in fall 2018 than in summer 2019 despite a significantly lower SWC in summer 2019 compared to early fall 2018. The increase in gas diffusivity in drier



soils explained the increase in soil CH_4 uptake measured in situ during moderate summer drought or experimental throughfall reduction (Epron et al. 2016; Fest et al. 2017).



However, very low SWC values could have subjected the methanotrophic bacteria to water stress in summer 2019 (van den Pol-van Dasselaar et al. 1998; Borken et al. 2006; von Fischer et al. 2009). We are aware that the potential CH_4 oxidation, assessed by incubation of intact cores, is not necessarily representative of the net methane flux that would be measured at the soil surface in situ. Nevertheless, Borken et al. (2006) reported a decrease in ex situ potential CH_4 oxidation during severe drought that was also reflected in the in situ seasonal pattern in soil CH_4 uptake. The higher CO_2 production measured at 20 °C in fall 2018 compared to summer 2019, the positive relationship between CH_4 oxidation and CO_2 production in summer 2019 and the results of the SEM analysis support the idea that severe summer drought was stressful for the microbial communities living in the top soil layer, including methanotrophic bacteria, at our site. At low SWC (low soil water potential), limited diffusion of soluble organic substrates and osmotic stress impair

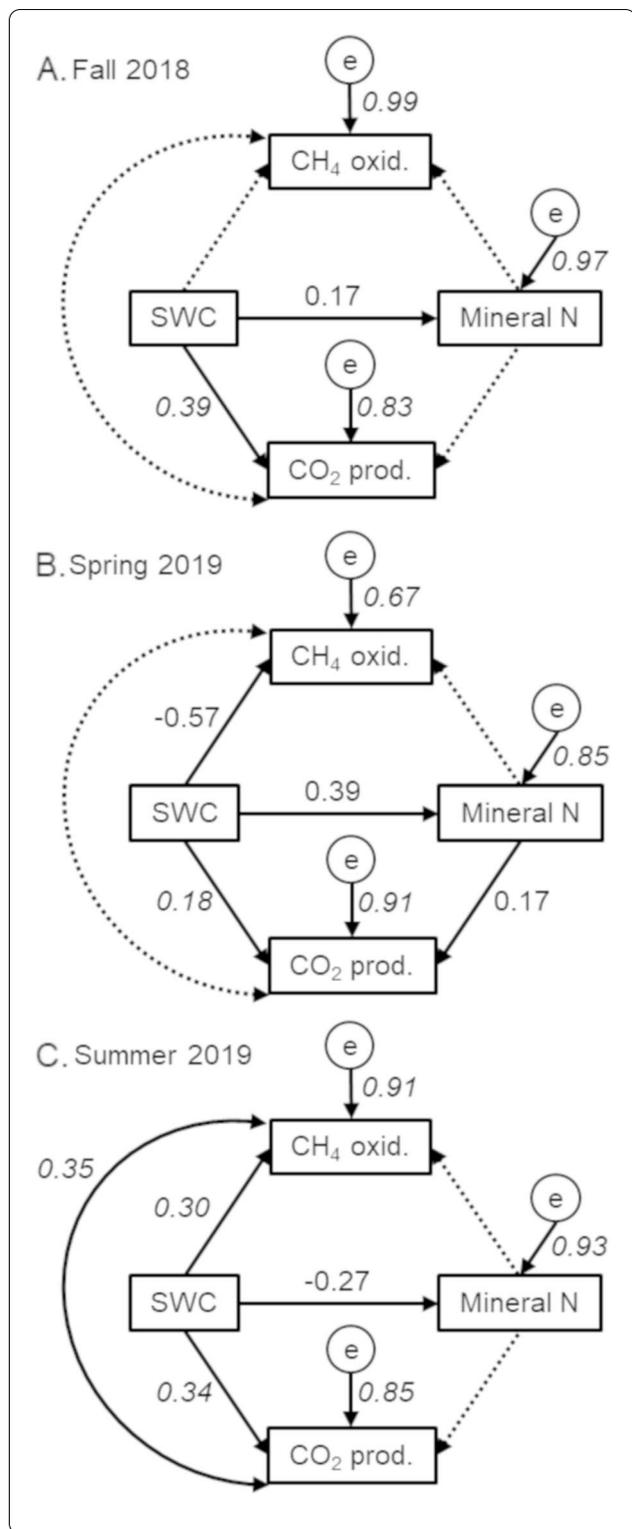


Fig. 5 Structural equation model analysis showing the direct influence of soil water content (SWC) and soil mineral nitrogen on potential CH₄ oxidation and CO₂ production in the top soil layer (intact soil cores), and the covariation of these two processes, in **A** fall 2018 ($\chi^2 = 0.011, p = 0.917; cfi = 1.000; rmsea = 0.000; srmr = 0.003$), **B** spring 2019 ($\chi^2 = 0.000, p = 0.998; cfi = 1.000; rmsea = 0.000; srmr = 0.000$) and **C** summer 2019 ($\chi^2 = 0.962, p = 0.327; cfi = 1.000; rmsea = 0.000; srmr = 0.031$). Solid straight arrows represent significant pathways ($p < 0.05$), and dotted arrows indicate nonsignificant pathways. Numbers adjacent to the arrows are standardised path coefficients (shown only for significant paths). The curved double-sided arrows represent the covariation between CH₄ oxidation and CO₂ production. **e** is the variance that is not explained by the predictors. Numbers of observations are 156 (12 samples in 13 stands) in **A** and **B** and 96 in **C** (12 samples in 8 stands)

diffuses better in air than in water, osmotic stress may be the main constraint in late summer and early fall. On the other hand, in early spring when soil water content is high and air-filled porosity low, gas diffusion was the limiting factor for CH₄ oxidation.

4.2 Variations in soil mineral nitrogen did not account for the variations in methane oxidation

Though soil mineral N is another important factor that could affect CH₄ oxidation since it is known to have both inhibitory and stimulating effects on methanotrophs (Goldman et al. 1995; Mochizuki et al. 2012), we did not observe any clear relation between mineral N content and potential CH₄ oxidation. Higher mineral N content in spring than in summer and early fall could be explained by higher N mineralisation in early spring along with low demand from trees (El Zein et al. 2011) and weaker mineralisation at the end of summer and early fall due to unfavourable edaphic conditions following a period of high consumption of belowground resources before the end of the growing season (Ellis 1974).

The weak negative relationship between potential CH₄ oxidation and mineral N content in summer 2019, when N content was the lowest and water stress the highest, suggests that unfavourable edaphic conditions in summer 2019 impacted both methanotrophic activity and nitrification. Nitrification is reduced during drought mainly because diffusion of NH₄ is limited in dry soils (Stark and Firestone 1995; Schimel 2018). Interestingly, NH₄ was always the dominant form of mineral nitrogen at our site; however, in the five stands that were measured both in spring and summer 2019, NH₄ represented 95% of the total mineral N in summer, and only 87% in spring. We therefore postulate that this weakly negative relationship between CH₄ oxidation and mineral N content resulted from a concomitant effect of soil drying on methanotrophic activity and nitrification in the top soil

microbial activity (Skopp et al. 1990; Stark and Firestone 1995; Moyano et al. 2012). Because methanotrophic bacteria gain their energy from the oxidation of CH₄, which

layer rather than from an inhibitory effect of mineral nitrogen on CH₄ oxidation. The lack of inhibitory effect of mineral N was consistent with a much lower mineral N content than in studies showing inhibition where it is usually related to the addition of nitrogen fertiliser (Seghers et al. 2003; Mochizuki et al. 2012).

4.3 Stand age has little influence on methane oxidation in the top soil layer and its putative drivers

Stand age alone did not explain variations of potential CH₄ oxidation between stands, but an additive model including both BA and stand age did, except during the 2019 summer drought. We hypothesised that both bulk density and soil water content would decrease with stand age due to the decompaction resulting from root growth (Bodner et al. 2014), the increase in soil organic matter (Boivin et al. 2009) and higher evapotranspiration in older stands than in younger stands (Barker et al. 2009). However, neither bulk density nor soil water content varied with stand age at our site. This lack of stand age effect on bulk density can be explained by the initial low bulk density in our young stands (between 0.8 and 1.1 kg dm⁻³) compared to previous study of Christiansen and Gundersen (2011) where bulk densities were higher (between 1.2 and 1.7 kg dm⁻³). These different densities could be explained by the land use: Christiansen and Gundersen (2011) focused on the afforestation of arable lands that had been compacted by agricultural machinery for many years, while our forest stands were naturally regenerated.

In contrast to a previous study on a tree plantation chronosequence on former agricultural land (Hiltbrunner et al. 2012), SWC was not related to stand age in our site. The reason is that, in contrast to forest plantations, all naturally-regenerated stands in our study had a closed canopy, even the youngest ones, due to an initial very high tree density, which decreased with time due to thinning and mortality. SWC was negatively related to the basal area (BA) of the stand. However, as already reported for other forest chronosequences (Roberts et al. 2001; Delzon and Loustau 2005), BA was not continuously increasing with stand age but reached a maximum value before 100 years and decreased thereafter.

Mineral N is thought to increase over time due to a decrease in N demand by trees, cumulative atmospheric N deposition or an increase in N mineralisation but, in contrast to our expectations, there was no effect of stand age on mineral N that could have, in turn, affected CH₄ oxidation. An increase in mineral N with stand age has been observed in Danish forests (Hansen et al. 2007; Christiansen and Gundersen 2011; Rahman et al. 2017). This increase was related to a decrease in N demand by trees after canopy closure, following a high demand for N

by the trees in their early growth stages when they were building up their N-rich canopy biomass compartments, and to an increase in N mineralisation with age. However, other studies have found a decrease in N mineralisation with stand age because N may be immobilised due to the accumulation of polyphenolic compounds (DeLuca et al. 2002). In contrast to the plantation chronosequence in the Danish study mentioned above, our young naturally-regenerated stands had a closed canopy. In addition, the development of an understorey composed of young hornbeams (30 to 100 cm tall) in our stands older than 86 years (stands 9 to 16) could have increased the N demand in these stands and counterbalanced the lower N demand of the older oak trees. It should also be noticed that nitrogen deposition in our study area (8 kg N ha⁻¹ in 2019 in a nearby beech stand belonging to French permanent plot network for the monitoring of forest ecosystems, RENE-COFOR) was lower than in the Danish forests (Hansen et al. 2007; Christiansen and Gundersen 2011).

4.4 Implication for the forest methane sink in the context of climate change and climate change mitigation

It has been suggested that young regrowth forests take up more CO₂ than old-growth forests while the latter store more carbon than the former (Schulze 2000; Stephenson et al. 2014; Pugh et al. 2019). However, the CH₄ sink function of forest soils has not been included in the debate about whether it is better to conserve old forests or harvest and regenerate them. We found that there was no effect of stand age on potential CH₄ oxidation in the top soil layer in a naturally regenerated oak-dominated deciduous temperate forest. Old stands consume as much atmospheric methane as younger stands and contribute equally to climate change mitigation. However, differences in both soil CH₄ uptake measured in situ and CH₄ oxidation measured ex situ have been reported between forest stands of different ages when forest regeneration occurred after a disturbance, such as severe forest fires, due to the effects of the disturbance on soil properties affecting gas diffusivity (Fest et al. 2015). The current increase in the use of heavy machinery for timber harvesting could alter the uncompacted nature of the soil in the future, potentially reducing methane oxidation in young stands in the next rotation. Frey et al. (2011) and Epron et al. (2016) have indeed reported a negative effect of soil compaction on in situ soil CH₄ consumption.

In the past 50 years, the strength and frequency of summer droughts have increased in central and southern Europe (Vicente-Serrano et al. 2014; Trnka et al. 2016). This trend could also become significant in western Europe in the coming years, as suggested by the severe summer droughts in the last 3 years (2018–2020, 45% less summer precipitation and 1.4° more for the

average summer temperature compared to the 30-year average based on data from the nearest weather station, Météo-France 2020). In the years to come, the frequency and severity of such droughts is likely to increase (Dai 2011; Trenberth et al. 2014; Spinoni et al. 2018; Grillakis 2019). The decrease in potential CH₄ oxidation that we observed in the top soil layer at the end of the very long dry summer in 2019 will presumably occur more frequently, thus reducing the CH₄ sink in temperate forest soils. While several studies have reported higher potential CH₄ oxidation in the top soil layer than deeper in the soil profile (e.g. Reay et al. 2005) and close agreements between ex situ measurements of potential CH₄ oxidation and in situ measurement of soil CH₄ uptake (Borken et al. 2006), CH₄ oxidation can happen across the whole aerobic soil profile (Fest et al. 2015). We cannot exclude that methanotrophic activity migrated deep into the soil profile during the dry summer, particularly because the high air-filled porosity and reduced oxidation in the upper soil may have favoured CH₄ diffusion in deeper layers. This might have at least partly counterbalanced the decreased activity in the top soil layer. As mentioned above, the potential CH₄ oxidation, assessed by incubation of intact cores, is not necessarily representative of the net methane flux that would be measured at the soil surface in situ. Further studies on the vertical distribution of soil CH₄ oxidation, and its seasonal variation, are needed.

In addition to severe summer drought, an increase in precipitation in late autumn, winter and early spring, and extreme precipitation events in summer despite drier conditions, would not only increase flood hazard but would also increase the frequency and duration of waterlogging episodes (Christensen and Christensen 2003; Dankers and Feyen 2009), reducing the soil CH₄ sink of temperate forest soils prone to waterlogging. Indeed, low gas diffusion in waterlogged forest soils is known to result in low in situ net methane uptake (Megonigal and Guenther 2008; Gundersen et al. 2012; Epron et al. 2016). Moreover, a recent study by Gatica et al. (2020) has shown that methanotrophic bacteria are more sensitive to warmer temperatures than methanogenic archaea. Wetter and warmer springs and flash floods in summer could favour methanogenic activity and decrease methane oxidation.

5 Conclusions

In this context of global warming and related extreme climatic events, our results emphasise that further studies should investigate the effects of long, severe summer droughts and waterlogging events have on the composition and activity of soil microbial communities, and how

the interactions between climate and microbial community affect atmospheric methane oxidation, and more generally soil functions and their related forest-ecosystem services.

Acknowledgements

We are grateful to J.-C. Olry, V. Rousselet and F. Bordat for their technical assistance in the field. We also acknowledge Dr N. Breda (INRAE) and C. Lemoine (ONF), who provided us with the age of the stands. We also thank A. Reichard and S. Bienaimé from the "Biogéochimie des Ecosystèmes Forestiers" laboratory who managed the measurement of the mineral N concentrations.

Code availability

The custom code generated during the current study is available from the corresponding author on reasonable request.

Authors' contributions

Conceptualisation: Nicolas Bras, Caroline Plain, Daniel Epron. Methodology: Nicolas Bras, Caroline Plain, Daniel Epron. Formal analysis and investigation: Nicolas Bras, Caroline Plain, Daniel Epron. Writing—original draft preparation: Nicolas Bras. Writing—review and editing: Caroline Plain, Daniel Epron. Funding acquisition: Caroline Plain, Daniel Epron. Supervision: Caroline Plain, Daniel Epron. All authors read and approved the final manuscript.

Funding

Nicolas Bras was supported by a grant from the French PIA project "Lorraine Université d'Excellence" (ANR-15-IDEX-04-LUE). UMR 1434 SILVA is supported by the French National Research Agency through the Laboratory of Excellence ARBRE (ANR-11-LABX-0002-01).

Availability of data and materials

The datasets analysed during the current study are available in the dorel repository (<https://dorel.univ-lorraine.fr/>), <https://doi.org/10.12763/B5ETNU>.

Declarations

Ethic approval and consent to participate

The authors declare that the study was not conducted on endangered, vulnerable, or threatened species.

Consent for publication

All authors gave their informed consent to this publication and its content.

Competing interests

The authors declare that they have no conflict of interest.

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Received: 11 October 2021 Accepted: 25 April 2022

Published online: 20 June 2022

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