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Controls of methane oxidation in dry streambeds

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ABSTRACT

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Despite advances in understanding methane dynamics in dry inland waters, the potential of dry riverbeds to act as sinks of methane, as soils do, and the controlling factors remain unclear. Here, we tested three main factors controlling methane oxidation in soils and freshwater ecosystems in sediments from a dry riverbed (decreasing in modulation degree): gravimetric water content (GWC), temperature, and light quality and intensity. We measured the rates of potential methane oxidation (PMO) along a gradient of GWC (1%, 5%, 8%, 10%, and 100%), temperature (10 ºC, 20 ºC, and 30 ºC) and light (in darkness, at photosynthesis-limiting (i.e., green) and photosynthesis-promoting (i.e., grow) light). Our results revealed that dry streambed sediments have the potential to oxidize methane. GWC, as the major controlling factor, followed a non-monotonic function, with the highest PMO of around 5% GWC. As the secondary control, temperature affected PMO from dry sediment only but not from 100% GWC sediment. PMO was the lowest at 10 ºC and highest above 20 ºC. Interestingly, light reduced PMO by 3–6× compared to dark conditions, and grow light reduced PMO by ~2× compared to green light. Our results indicate that there will be day–night and seasonal variations in methane oxidation from dry riverbeds as a function of temperature, GWC and light, and between reaches, depending on the canopy cover and associated riverbed shading. Overall, our results highlight the potential of dry riverbeds to act as sinks of methane from the atmosphere.

KEY WORDS: intermittent rivers, carbon cycling, biogeochemistry

RESUMEN

Controles de la oxidación del metano en lechos fluviales secos.

A pesar de los avances en la comprensión de la dinámica del metano en aguas continentales secas, sigue sin estar claro el potencial de los lechos fluviales secos para actuar como sumideros de metano, al igual que los suelos, y los factores que los controlan. En este trabajo se analizaron tres factores principales que controlan la oxidación del metano en suelos y sedimentos de agua dulce en sedimentos de un lecho fluvial seco (con un grado de modulación decreciente): el contenido gravimétrico de agua (GWC), la temperatura y la calidad e intensidad de la luz. Se midieron las tasas de oxidación potencial de metano (PMO) a lo largo de los gradientes de GWC (1%, 5%, 8%, 10% y 100%), temperatura (10 ºC, 20 ºC y 30 ºC) y luz (en la oscuridad y con luces que limitan la fotosíntesis (es decir, verdes) y que promueven la fotosíntesis (es decir, de crecimiento)). Nuestros resultados revelaron que los sedimentos de lechos fluviales secos tienen potencial para oxidar metano. La GWC, como principal factor de control, siguió una función no monotónica, con la PMO más alta en torno al 5% de GWC. Como control secundario, la temperatura afectó a la PMO del sedimento seco solamente pero no del 100% GWC. La PMO fue la más baja a 10 ºC y la más alta por encima de

20 ºC. Curiosamente, la luz redujo la PMO en 3-6× en comparación con las condiciones de oscuridad, y la luz de crecimiento redujo la PMO en ~2× en comparación con la luz verde. Nuestros resultados indican que habrá variaciones diurnas y nocturnas y estacionales en la oxidación de metano de los lechos secos de los ríos en función de la temperatura, el GWC y la luz, y entre tramos, dependiendo de la cobertura del bosque de ribera y el sombreado asociado del lecho del río. En conjunto, nuestros resultados resaltan el potencial de los cauces secos de los ríos para actuar como sumideros de metano de la atmósfera..

PALABRAS CLAVE: ríos intermitentes, ciclo del carbono, biogeoquímica.

INTRODUCTION

While freshwater ecosystems are responsible for about half of global methane (CH_4) emissions to the atmosphere (Rosentreter et al., 2021), the roles of streams and rivers remain unclear (Rocher-Ros et al., 2023), and even more when those systems dry out (Marcé et al., 2019; Paranaíba et al., 2022; Silverthorn et al., 2023). Many streams and rivers worldwide experience periods of drying (i.e., absence of surface water flow) (Messager et al., 2021), which in turn may alter their CH_4 dynamics. Compared to nearby uphill soil, dry riverbeds emit ~30× more CH_4 into the atmosphere (Paranaíba et al., 2022) but with large variability, including influx from the atmosphere into the dry riverbed. In fact, about 25% of the studied cases reported a net influx of atmospheric methane (i.e., methane oxidation; Paranaíba et al., 2022). For such reasons, estimates of CH_4 emissions from riverine systems are an important source of uncertainty in the global CH_4 budget (Saunois et al., 2020), and given the global prevalence of river intermittence, i.e., drying and rewetting (Messager et al., 2021), the contribution of intermittent systems might be of relevance. In dry riverbeds, the expansion of the oxic layer of the sediment promotes aerobic processes such as aerobic methane oxidation (hereafter referred to as methane oxidation or methanotrophy Koschorreck, 2000; Jäckel et al., 2001). Yet the mechanisms controlling methane oxidation in dry riverbeds are not fully understood (Paranaíba et al., 2022).

Dry riverbeds have been proposed to biogeochemically behave like early stage soils (Arce & Mendoza-Lera et al., 2019) so that we can use studies from soils to understand their methane oxidation dynamics. Soils are important sinks of methane contributing up to 33.5±0.6 Tg CH_4 per year (Murguia-Flores et al., 2018), corresponding to about 6% of the global methane budget (576 Tg CH_4 per year, 2008–2017; Saunois et al., 2020). Factors that modulate methane oxidation, in both soils and submerged sediments, may act i) indirectly, affecting the diffusion (and concentration) of the substrate (CH_4 and oxygen), and/or ii) directly, affecting the methane oxidizing community in terms of composition and activity (King & Blackburn, 1996; Le Mer & Roger, 2001; Bastviken, 2009). In this work, we considered three factors controlling methane oxidation with decreasing modulation degree: water availability, temperature, and light. The primary factor—water availability—influences both diffusion of substrates and activity of oxidizing community. Diffusion is faster in air than in water and across interfaces; therefore, the water content in the sediment will condition the diffusion of CH_4 and oxygen (King & Adamsen, 1992; Schnell & King, 1996). On the other hand, low water availability results in hydric stress in microbial communities (Schnell & King, 1996; Ball et al., 1997). The interplay between the direct and indirect effects of water content in soils results in a non-monotonic function of methane oxidation, as water content diminishes and the volume of oxidized soil increases (Striegel et al., 1992; Schnell & King, 1996; Torn & Harte, 1996; Le Mer & Roger, 2001). At high water content, methanotrophy is limited by the diffusion of substrates; at intermediate levels of water content, methanotrophy is maximum due to a faster supply of methane and oxygen through air diffusion; and at low water content, microbial activity is impaired by hydric stress (Collet et al., 2015; Ho et al., 2016). In fact, as a function of moisture, soils may behave as sinks or sources of methane to the atmosphere (Le Mer & Roger, 2001) and similar patterns could therefore be expected from dry riverbed sediments. Arce et al.

(2021) observed, in laboratory incubations of river sediment, that CH_4 emissions decreased with increasing sediment-drying time. Thus, streams may have the potential as well to act as CH_4 sinks during the dry periods contrasting their net CH_4 emissions during flowing periods as observed in permanent flowing systems (Rosentreter et al., 2021; Rocher-Ros et al., 2023).

The secondary factor—temperature—also has direct and indirect effects on microbial communities. Diffusion and metabolic rates are temperature-dependent (King & Adamsen, 1992; Reddy et al., 2019). The interplay between the direct and indirect effects of temperature on methane oxidation, however, varies between aquatic and terrestrial ecosystems (Reddy et al., 2019). In wetland soils, methane oxidation was found to be less sensitive to temperature than other processes, with the temperature coefficient (Q_{10}) varying from 1.4–2.1, while other processes, such as methanogenesis, ranged from 1.5 to 28 (Segers, 1998). Between 4 ºC and 30 ºC, inundated sediments showed that temperature had a limited effect on CH_4 oxidation (Duc et al., 2010). While in soils, Reddy et al., (2019) reported that temperature is a critical factor affecting CH_4 oxidation. They reported an increase in oxidation from 6 ºC to 30 ºC, which then decreased to zero at 70 ºC. Therefore, it is unclear what could be expected from dry riverbed sediment. Still, diurnal temperature fluctuations increase in dry riverbeds due to reduced thermal mass, i.e., reduced volumetric heat capacity compared to wetted riverbeds (Larned et al., 2010), thereby potentially affecting methanotrophy and emission dynamics from dry riverbeds, as observed in soils (Reddy et al., 2019).

Finally, light is the tertiary factor influencing methane oxidation. The effect of light intensity on methane oxidation has been less studied, and the mechanisms remain poorly understood (King, 1990a; King & Adamsen, 1992; King et al., 1996; Dumestre et al., 1999; Sugimoto, 2005; Murase & Frenzel, 2007; Bastviken, 2009; Shelley et al., 2017). Light can affect methane oxidation indirectly, through increased availability of oxygen from primary production (King, 1990a; Oswald et al., 2015), and/or directly, by reducing the activity of methane monooxygenase enzyme (Bédard & Knowles, 1989; Dumestre et al., 1999). Few laboratory studies on pelagic communities have revealed a decrease in methane oxidation as light intensity decreased (Dumestre et al., 1999; Murase & Sugimoto, 2005). Similarly, in streambeds, Shelley et al. (2017) reported higher methanotrophy in shaded reaches than in unshaded ones. In contrast, in sediments with algal mats from a wetland and a pond, King (1990a, 1990b) reported an increase in CH_4 oxidation with light intensity and attributed it to increased oxygen availability from primary production. To date, the available studies are too sparse to generalize whether light intensity positively or negatively affects methane oxidation and whether this it may occur through increased photosynthetic activity. Differences in the effect of light intensity could also be attributed to the quality of the incident light, i.e., its spectral composition, which might also influence methane oxidation. For instance, if the interaction is through photosynthetic activity, then methane oxidation under unfavorable light conditions for photosynthesis (e.g., green light) should be lower than under optimal photosynthesis-promoting conditions (i.e., grow light). This could be highly relevant for understanding CH_4 emission patterns from dry rivers with open and closed canopy cover in temperate climates, where changes in light quality might boost or dampen photosynthesis in the sediment, and thereby CH_4 emissions, spatially and seasonally.

The goal of this study was to determine the potential of dry riverbeds in oxidizing CH_4 and the influence of three major controlling factors reported in soils and freshwater-inundated systems: water content, temperature, and light (intensity and spectral composition). We hypothesized that: (i) in response to drying, methane oxidation will follow a unimodal function with the highest rates at intermediate water content; (ii) in response to temperature, methane oxidation from inundated (wet) sediment will not increase with temperature, while from dry sediments will increase with temperature; (iii) in response to light intensity, methane oxidation, regardless of water content, will be higher under light compared to dark conditions; and (iv) in response to light spectral composition (with the same intensity), methane oxidation will be higher under photosynthesis-promoting (grow) light than under photosynthesis-limiting (green) light.

METHODS

Sediment sampling and preparation

Sediment was collected from the Queich River in Offenbach an der Queich, Germany (49.2026 °N, 8.1881 °E) in March 2022. Sediments were sieved in situ into very coarse to fine sand (6.3–0.2 mm; Wentworth, 1922). About 1 kg of sediment was collected and transported, submerged in river water to the lab, where the sediment was enriched with five crushed alder leaves (*Alnus glutinosa*) per kg of sediment (approx. 0.12 mg g^{-1} of sediment). The enriched sediment was left for acclimation at 20 ºC under ambient (daily) light for a week prior to the measurements (Mendoza-Lera, 2017). A 5 cm thick water column of river water was maintained over the sediment to allow for continuous aeration with an air pump.

Experimental setup

The experimental setup aimed at investigating potential methane oxidation (PMO) as a proxy for methanotrophy (following Bodmer et al., 2020) along gradients of sediment water content and temperature, both under dark and diverse light conditions, simulating naturally occurring conditions under controlled laboratory conditions (Fig. 1). Each treatment was performed by incubation of 10 mL of sediment in pre-weighed 100 mL glass vials, in sets of four replicates, for a week. Each replicate vial was first crimp-sealed, and then the headspace was gas-enriched by adding 120 µL of pure CH_4 gas (1710 RN, Hammilton) using a gas-tight syringe (target mass, 70 µg of CH_4). In parallel control vials for each treatment were incubated without sediment to correct for leakage and changes in CH_4 concentration due to abiotic factors. The results from these control

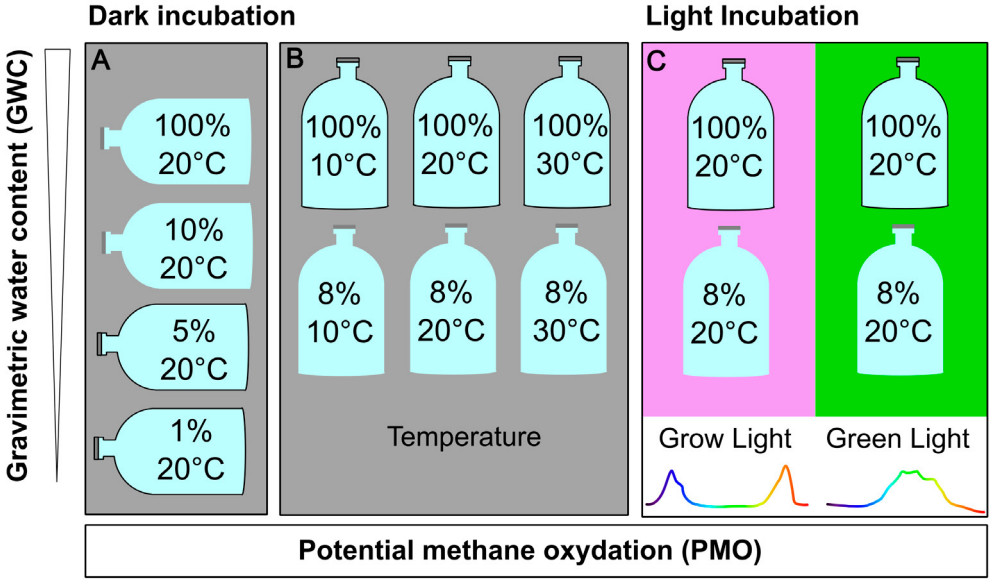

Figure 1. Overview of the experimental setup. The sediment incubation treatments included dark incubations with a gradient of gravimetric water content (GWC) at constant temperature (A), dark incubations of wet and dry sediment over a gradient of temperatures (B), as well as light incubation at constant temperature with both plant grow (photosynthesis promoting) light and green (photosynthesis-limiting) green light (C). All incubations were performed in four replicate vials except for treatment B at 10°C (three replicates). Note that the spectral distribution of the light sources is provided in an exemplary fashion (see SI Fig. 2 for details). *Visión general del diseño experimental. Los tratamientos incluyeron incubaciones oscuras con un gradiente de contenido gravimétrico de agua (GWC) a temperatura constante (A), incubaciones oscuras de sedimento saturado de agua y seco sobre un gradiente de temperaturas (B), así como incubación con luz a temperatura constante tanto con luz de crecimiento vegetal (promotora de la fotosíntesis) como con luz limitadora de la fotosíntesis(verde) (C). Todas las incubaciones se realizaron en viales (cuatro réplicas, excepto el tratamiento B a 10°C con tres réplicas). La distribución espectral de las fuentes de luz se proporciona a modo de ejemplo (SI Fig. 2 para más detalles).*

vials revealed that the mean change in concentration over 168 h was within the same order of magnitude as the detection limit of the method (6.7 vs. 4.5 ppm), and the coefficient of variation between replicates was below the average reproducibility of the closed-loop injectors (5.9%) (Wilkinson et al., 2018). Based on this, we can reasonably assume that no leakage and/or abiotic effects on the CH_4 concentrations were detected.

The drying treatment (Fig. 1A) encompassed sediment samples with four levels of gravimetric water content (GWC), 1%, 5%, 10%, and 100% (wet), which were incubated in the dark under constant 20 ºC in a climate-controlled room and shaken daily to ensure mixing. The level of GWC (quantified as the mass of water per mass of dry sediment) was determined from parallel samples until the desired GWC was reached. These ranges were selected based on Schreckinger et al. (2021), who reported intermediate microbial activities within 30 days of drying, with GWC ranging from 10% to 1%. A drying period of up to 30 d was identified as the most frequent zero-flow (i.e., drying) duration among natural flow regimes with occurrence or recurrence of dry phases (Kennard et al., 2010).

The temperature treatment (Fig. 1B) included samples with 8% (i.e., dry) and 100% (i.e., wet) GWC incubated in the dark at 10 °C, 20 °C and 30 ºC, respectively. The value of 8% GWC as the dry treatment was based on measurements from the GWC drying treatment measurement (as described above). There, we observed that the tipping point of the effect of drying happened between 5% and 10% GWC, with 8% representing a practical midpoint target within such range. Points between the effects of wet and dry sediments. To ensure constant temperature, the 10 ºC incubation was conducted in an incubation bath (F12-ED, Julabo), while the 30 ºC vials were placed inside a drying cabinet (FD-S 56, Binder). The 20 ºC incubations were performed in a climate-controlled room.

For the light quality treatment (Fig. 1C), we used samples with 8% (i.e., dry) and 100% GWC (i.e., wet) incubated at 20 ºC under constant light (no day-night cycles) for a week. One set of vials was exposed to a typical (blue–red) plant-growing light to boost potential autotrophic activity, while the other one was only exposed to green light, to minimize potential autotrophic activity (Kang et al., 2016). Green light was created using three conventional LED bulb spectra filtered through green foil. The spectra of the respective lights (Fig. S1, Supplementary information, available at https://www.limnetica.net/en/limnetica) were determined using an inexpensive self-built spectrometer based on the open-source Theremino design (https://www.theremino.com); details are provided in the supplementary information, Text 1, Fig. S1 and Fig. S2 (available at https://www.limnetica.net/en/limnetica). To rule out artifacts due to variations in light intensity, the total photosynthetically available radiation reaching the surface of the vials from the grow light was measured with a SQ-520 Full-Spectrum Quantum Sensor (Apogee instruments Inc., USA) and set to 200 µmol photon m^{-2} s^{-1} to match the maximum PAR deliverable by the green light setup. Computer fans were installed to minimize any light-dependent warming of the vials above 20° C.

At the end of each incubation, the vials were opened and dried at 60 ºC for 48 h for dry weight (DW) determination.

Determination of PMO rates

Headspace CH_4 concentrations were measured every 24 h for the first three days and then each 48 h over a week using an ultra-portable laser absorption spectrometer (UGGA, model 915-0011, Los Gatos Research Inc., California, USA). The measurements followed the closed-loop injection approach of (Wilkinson et al., 2018). Here 100 µL of headspace sample were withdrawn from the vial using a gas-tight syringe (1710 RN, Hammilton), and injected into the closed-loop system. The CH_4 concentration in the sample (X_{sample}, in ppm) was then calculated considering the relationship between the injected sample volume (V_{sample}, in mL), the total loop internal volume (V_{loop}, in mL) as follows.

$$X_{sample} = \frac{V_{loop}}{V_{sample}} \Delta X + X_{eq} \quad (1),$$

where Δx represents the difference between the background concentration in the loop prior to injection (X_0) and the equilibrium concentration reached after injection (X_{eq}). The volume of the closed loop was estimated using Equation 1 by injecting a standard gas (Messer Industriegase GmbH, Germany) at a known concentration of 5052 ppm. Estimates of V_{loop} were made before and after each series of measurements, with three replicates. The mean of the resulting six V_{loop} determinations was then used to calculate the sample concentrations of the respective series of measurements.

The amount of CH_4 (mol) in each sample vial was quantified as following Wilkinson et al. (2018). PMO rates were calculated by fitting the data to a linear model over the first three days of incubation following Bodmer et al. (2020) and Shelley et al. (2014) and expressed as µg CH_4/ mgDW day.

Data analysis

We report all values as mean and standard deviation. We ran two-way analysis of variance (ANOVA) (one-way ANOVA for GWC) to test for the effect of each treatment for each test following post hoc tests; when needed, data were log-transformed to ensure normality. Headspace concentrations below the detection limit of 4.5 ppm were replaced with zero (Wilkinson et al., 2018). We considered tests significant at $p < 0.05$. We ran all statistical analyses in R (version 4.1.3; R Core Team, 2022).

RESULTS

Overall, the rates of potential methane oxidation (PMO) increased as the gravimetric water content (GWC) decreased, up to a maximum at 5% GWC, and then non-monotonically decreased from 5% to 1% GWC (Fig. 2) (one-way ANOVA: $F_{3, 36} = 1031$, $p < 0.001$). Above 8%, till 100% GWC, methane oxidation remained constant, about 10× lower than that observed for dryer sediments (Fig. 2).

Under different temperatures, the overall PMO was between ~3 and ~6× higher under dry (8% GWC) conditions than under wet (100% GWC) conditions (Fig. 3) (two-way ANOVA:

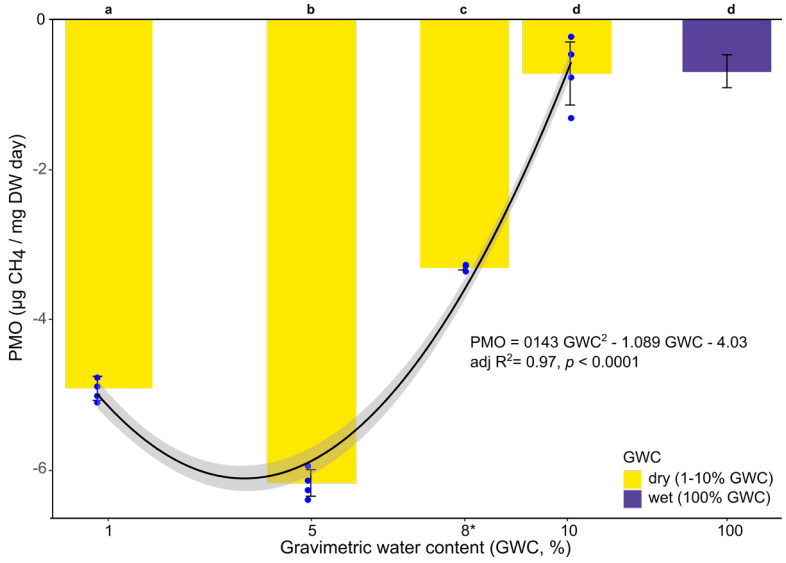

Figure 2. Potential Methane Oxidation (PMO) along a Gravimetric Water Content (GWC) gradient. Letters indicate significant differences (adjusted p <0.05) between levels of GWC from post hoc following ANOVA. *Note that the values at 8% correspond to the measurements performed at 20ºC for the temperature treatment. The polynomial function represents the change of PMO as a function of GWC. *Oxidación potencial de metano (PMO) a lo largo de un gradiente de contenido gravimétrico de agua (GWC). Las letras indican diferencias significativas (*p *ajustada <0.05) entre niveles de GWC a partir de ANOVA post hoc. *Nótese que los valores al 8% corresponden a las mediciones realizadas a 20ºC para el tratamiento de temperatura. La función polinómica representa el cambio de PMO en función del GWC.*

$F_{1, 60}$ = 77 043, p <0.0001). Under wet conditions, PMO did not vary as a function of temperature; under dry conditions, PMO was approximately ~1.7× lower at 10 ºC than at 20 ºC or 30 ºC (Fig. 3; two-way ANOVA: $F_{2, 60}$ = 204.5, p <0.0001).

The effect of light on PMO was detected regardless of GWC (Fig. 4, two-way ANOVA: $F_{1, 66}$ = 38 038, p <0.0001). Overall, the PMO was higher under dark conditions than under any of the two lights (Fig. 4; $F_{2, 66}$ = 22 107, p <0.0001). For dry sediment, the PMO was ~6× and ~3× lower for grow and green lights, respectively, than in the dark at the same temperature (Fig. 4). While for wet sediment, it was ~12× and ~5× higher in darkness than under grow and green lights, respectively (Fig. 4). The differences between grow and green light were comparable for both dry and wet sediments and were ~2× higher for green light than for grow light (Fig. 4).

DISCUSSION

Our results show that sediments from dry riverbeds have the potential to act as sinks of CH_4. This is in line with the findings of Paranaíba et al. (2022) from a global survey of CH_4 fluxes from dry aquatic sediments. The authors reported a net influx of CH_4 (i.e., methane oxidation) in about 25% of the studied cases. We tested the effects of three major factors controlling methane oxidation from soils and freshwater sediments (King et al., 1996; Bastviken, 2009) (with a decreasing degree of modulation) on dry riverbed sediment: water availability (i.e., GWC), temperature, and light intensity and quality. Overall, these three factors significantly modulated PMO and, according to their relevance, with different intensities.

In dry riverbed sediments, comparable to that observed in soils, the water content in the sediment

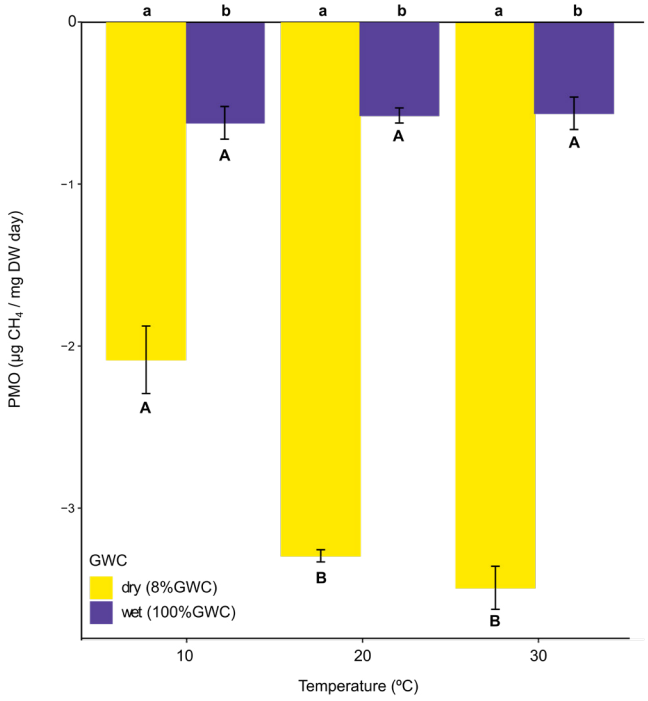

Figure 3. Potential Methane Oxidation (PMO) along a temperature gradient for sediment at 8% (dry) and 100% (wet) Gravimetric Water Content (GWC). Lower case letters indicate significant differences (adjusted p <0.05) within temperature levels from post hoc following ANOVA. Upper case letters indicate significant differences (p <0.05) within GWC among temperatures following ANOVA. *Oxidación Potencial de Metano (PMO) a lo largo de un gradiente de temperatura para sedimentos al 8% (seco) y 100% (saturado) de Contenido Gravimétrico de Agua (GWC). Las letras minúsculas indican diferencias significativas (*p *ajustada <0.05) dentro de los niveles de temperatura a partir de ANOVA post hoc. Las letras mayúsculas indican diferencias significativas (*p *<0.05) dentro del GWC entre temperaturas tras ANOVA.*

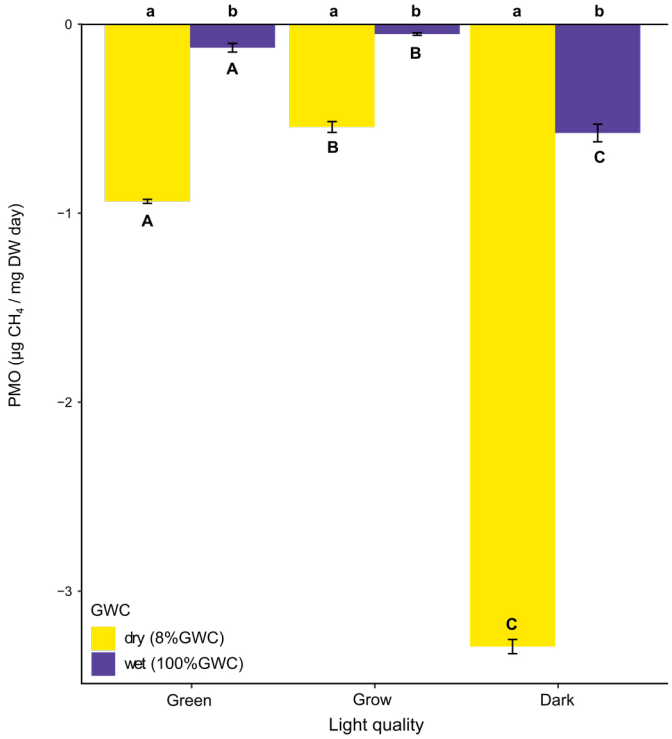

Figure 4. Potential Methane Oxidation (PMO) at three light conditions: two different light qualities (Green and Grow) with the same intensity (200 µmol photon m^{-2} s^{-1}) and Dark conditions for sediment at 8% (dry) and 100% (wet) Gravimetric Water Content (GWC). Lower case letters indicate significant differences (adjusted p <0.05) within light quality levels from post hoc following ANOVA. Upper case letters indicate significant differences (adjusted p <0.05) within GWC among light qualities from post hoc following ANOVA. *Oxidación Potencial de Metano (PMO) en tres calidades de luz: dos calidades diferentes (Verde y Crecimiento) con la misma intensidad (200 µmol fotón m^{-2} s^{-1}) y condiciones de Oscuridad para sedimento al 8% (seco) y 100% (saturado) de Contenido Gravimétrico de Agua (GWC). Las letras minúsculas indican diferencias significativas (*p *ajustada <0.05) dentro de los niveles de calidad de la luz a partir del ANOVA post hoc siguiente. Las letras mayúsculas indican diferencias significativas (*p *ajustada <0.05) dentro del GWC entre calidades de luz a partir de ANOVA post hoc.*

was the major driver of PMO following a non-monotonic function, as observed in soils with the highest rates at intermediate gravimetric water content levels (about 5%; Striegl et al., 1992; Schnell & King, 1996; Torn & Harte, 1996; Le Mer & Roger, 2001). This pattern likely resulted from the combined effects of water availability and faster diffusion in air, compared to water (Schnell & King, 1996), and was consistent regardless of the treatment applied. It is worth noting that at higher GWC than those in our study (i.e., between 10–100% GWC), different patterns might be observed. Overall, in a dry riverbed, the water content will change in time and space, and so will its potential to act as a sink of methane. As the flow contracts, areas that dry faster or earlier might act as hot moments compared with those that dry slower (Gómez-Gener et al., 2021). This idea can also be transferred to the banks of perennial rivers that are inundated as a function of discharge oscillations. The riverbanks could therefore act as sinks of methane, while the thalweg would act as a source. For example, Bednařík et al. (2019) determined methane oxidation from riverbank sediments with 100% GWC freshly exposed to air (within hours) and reported higher oxidation rates from those areas of the banks more frequently exposed, than for those in the thalweg, which were inundated for longer periods. This could, in turn, be modulated by the microbial communities, so that communities exposed to frequent drying might have a higher potential to oxidize methane than those that are less exposed (Goldman et al., 2017; Arce & Mendoza-Lera et al., 2019).

In soils, methane oxidation has been reported to be highest between 20 and 40 ºC (King & Adamsen, 1992; Reddy et al., 2019), while in inundated sediments, methane oxidation was reported to be mostly independent of temperature (Duc et al., 2010). Comparably, in our incubations, PMO was affected by temperature under dry conditions, with the highest at both 20 ºC and 30 ºC, and lowest at 10 ºC, but showed no effect under wet conditions. Thus, as proposed, the effect of temperature is secondary compared to water availability and is the strongest below 10 ºC. It is noteworthy that an even stronger reduction can be expected for dry sediments at lower temperatures. As observed by Reddy et al. (2019), PMO at 6 ºC, <0.002 µg/mgDW day, was about an order of magnitude lower than at 10 ºC. For the wet sediment at 6 ºC, in contrast, no significant changes may be observed; see Duc et al. (2010). This highlights the biogeochemical similarities between dry riverbeds and soils, compared to inundated sediments (Arce & Mendoza-Lera et al., 2019). Compared to other microbial processes (e.g., methanogenesis), the effect of temperature on methane oxidation is substantially lower (King & Adamsen, 1992; Segers, 1998). The Q_{10} values for wetland sediment, from the extensive study of Segers (1998), ranged from 1.5 to 28 for methanogenesis (n=1000) but were limited to 1.4–2.3 for methanotrophy (n=300). The proposed explanations for these different sensitivities are related to the low temperature sensitivity of the enzymes involved (Brazeau & Lipscomb, 2000). While our experimental setup cannot rule out such mechanisms, it does suggest that temperature sensitivity might be modulated by water availability and potentially through community differences. Given the high methane concentrations in our setup, diffusion was not the limiting factor for PMO, and methane oxidizers capable of being active under low water availability are likely more sensitive to temperature.

The effect of light on methane oxidation can be indirect through oxygen concentration variability associated with photosynthetic activity and/or through direct effects on methane monooxygenase enzyme (Bédard & Knowles, 1989; King, 1990a; Dumestre et al., 1999; Oswald et al., 2015; Shelley et al., 2017). Previous research in wetlands and inundated streambeds has reported that light can reduce methane oxidation rates (King, 1990a; King, 1992; Dumestre et al., 1999; Shelley et al., 2017); however, it remains unclear whether the effect of light is just related to the intensity or whether the spectral composition (i.e., light quality) would also affect methanotrophy (Dumestre et al., 1999). Our results reveal first that, at 20 ºC, 200 µmol photon m^{-2} s^{-1} of light reduces PMO between 3 and 4× compared to dark conditions. This is in line with King (1990a and 1992), who reported a decrease of 2.5× at the same light intensity for wetland sediment, but contrasts Murase & Sugimoto (2005), who reported inhibitory effects at much lower light intensities (23 µmol photon m^{-2} s^{-1}). Under the same light intensity, light quality had a distinct effect on PMO, with ~2× higher PMO under green light (photosynthesis-limiting) compared to grow light (photosynthesis-promoting), regardless of water content. Our results not only provide further evidence for the overall inhibitory effect of light on PMO but also on the potential role of sediment primary production on PMO. While rates of gross primary production were not explicitly investigated in our study, the use of both photosynthesis-promoting (grow light) and photosynthesis-limiting (green light) lights enabled a direct comparison of PMO with and without photosynthetic activity (Kang et al., 2016). Our results suggest that photosynthetic activity in sediments might have a detrimental effect on methanotrophy. Interestingly, in the water column of a stratified lake, Oswald et al. (2015) reported that light promotes methane oxidation compared to dark conditions. They proposed that the oxygen released by primary production promoted methanotrophy. In fact, Oswald et al. (2015) observed high methanotrophy under light conditions at the oxycline, but, above it, with higher oxygen concentrations, methanotrophy levels were lower. Compared to our setup, in which oxygen was available, the results from Oswald et al. (2015) suggest that, while under low-oxygen conditions, light might stimulate methanotrophy through primary production, and under oxic conditions, light has a negative effect on methanotrophy. Therefore, the effects of light on methanotrophy might be modulated by oxygen availability. At the reach scale, light dependence

influences not only day/night CH_4 emissions from i) both dry and inundated sediments, as observed for carbon dioxide (Attermeyer et al., 2021), and from ii) reaches with varying canopy covers, but also CH_4 emissions throughout the seasons (in temperate sites).

While permanent rivers and non-permanent rivers during flowing phases are net emitters of CH_4 (Rosentreter et al., 2021), their dry phase could contribute to the global CH_4 sink. Overall, the capacity of a given dry reach to act as a sink of CH_4 will ultimately depend on the proportion of the riverbed under oxic and anoxic conditions. CH_4 produced in deeper, anoxic layers of the riverbed may override the oxidizing activity happening in oxic areas. However, it is worth noting that in rice field soils and wetlands, about 90% of CH_4 produced in anaerobic areas is oxidized before reaching the atmosphere (King, 1990a,b; Le Mer & Roger, 2001). Subsurface hydrology, such as hyporheic flow or groundwater table oscillations, strongly influence these dynamics (Gómez-Gener et al., 2021), which are modulated by seasonal and daily changes in temperature and canopy cover. Understanding the spatial and temporal variability of sources and sinks of CH_4 along fluvial networks will improve predictions of the contributions of aquatic ecosystems to watershed carbon cycling (Bretz et al., 2021), especially in light of projections of longer dry periods (Beniston et al., 2007; Huang et al., 2015).

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DATA AVAILABILITY

Data can be found on Pangea: https://doi.org/10.1594/PANGAEA.973627

AUTHOR CONTRIBUTIONS

C.M.L.: Conceptualization, Methodology, Data curation, Writing, Original draft preparation, Visualization, Writing- Reviewing and Editing; J.L.: Conceptualization, Data curation, Writing, Original draft preparation, Writing- Reviewing and Editing; L.R.: Conceptualization, Methodology, Writing- Reviewing and Editing

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