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Hydrological and temperature controls on CO₂ and CH₄ exchange between a mid-altitude mountain peatland and the atmosphere

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SUMMARY

The aim of the present study is to understand the variability and the environmental factors controlling the fluxes of carbonaceous greenhouse gases (GHGs), methane (CH₄) and carbon dioxide (CO₂) between a temperate *Sphagnum*-dominated mid-altitude mountain peatland and the atmosphere. We conducted monthly measurements of GHG fluxes over 20 months using the chamber method. Specifically, we assessed the effects of (1) air temperature and (2) water level (WL) on GHG emissions. Open Top Chambers (OTC) were used to simulate a warming effect by passive heating of the air above the soil. To assess the effect of WL, we studied a hydrological gradient along a 35 m long transect from a near-surface “WET” area, through an “INTER” area with an intermediate WL, to a “DRY” area with a lower WL. The WET area featured a higher cover of *Sphagnum* species while the vegetation cover in the DRY area contained more vascular plants. Although all plots showed the same seasonality of GHG fluxes, considerable variability was observed among them. Raising the temperature using OTCs, which increased annual average air temperature by 0.2 °C to 0.6 °C, did not significantly affect CH₄ and CO₂ respiration (Reco) fluxes. In contrast, hydrological conditions played an important role in explaining flux variability. CH₄ fluxes were significantly higher in the WET and INTER areas (median [95 % CI] values: 17.5 [14.2, 29.0] and 20.0 [14.8, 30.4] nmol m⁻² s⁻¹) compared to the DRY area (3.4 [1.9, 9.4] nmol m⁻² s⁻¹) during all hydrological periods, i.e., humid spring, humid summer and dry summer. Reco did not vary significantly along the hydrological gradient overall, but the fluxes were lower in the WET area under humid spring (0.4 [0.3, 0.6] μmol m⁻² s⁻¹) and summer (1.7 [1.25, 2.75] μmol m⁻² s⁻¹) conditions compared to the DRY area (1.6 [1.3, 2.0] μmol m⁻² s⁻¹ in spring and 3.8 [2.7, 4.6] μmol m⁻² s⁻¹ in summer). Conversely, greater fluxes (by ~0.5 μmol m⁻² s⁻¹) were observed in the WET area during summer drought. Given that Reco emissions are expected to be higher during droughts in the DRY area, we hypothesise a possible threshold effect, such as inhibition of phenoloxidase activity and/or other enzymatic activities, which would limit organic matter decomposition. Moreover, increasing WL in the WET and INTER areas led to a drastic drop in gross primary production (GPP) corresponding to *Sphagnum* immersion.

KEY WORDS: chambers, greenhouse gas, hydrology, Open Top Chamber, *Sphagnum*

INTRODUCTION

Greenhouse gas (GHG) exchanges between terrestrial surfaces and the atmosphere are spatially and temporally heterogeneous due to the large variability of ecosystems and human land uses (Luyssaert *et al.* 2012, Premke *et al.* 2016). Peatlands, which occupy only a small proportion (~3 %) of the global land area, constitute an

outstanding carbon stock of about one-third of total soil organic matter (Yu *et al.* 2010, Xu *et al.* 2018, Nichols & Peteet 2019). As a result, GHG exchanges between peatlands and the atmosphere have played a significant role in climate regulation during the Holocene, through the sequestration of atmospheric CO₂ (Yu 2011, IPCC 2013). The current and future carbon exchanges between peatlands and the atmosphere are therefore crucial for evaluating their

carbon sink or source strength (Humpeñöder *et al.* 2020, Loisel *et al.* 2021, Tanneberger *et al.* 2021).

In peatlands, the two main GHGs (CO₂ and CH₄) are produced or consumed by biogeochemical processes which are directly and indirectly influenced by water level (WL) and soil temperature (Moore & Dalva 1993, Lafleur *et al.* 2005, Abdalla *et al.* 2016, Samson *et al.* 2018, Evans *et al.* 2021). These two factors play key roles in controlling the biotic participants (vegetation, microorganisms) involved in carbon dynamics and, as a result, have become a major focus for research (Andersen *et al.* 2013, Jassey *et al.* 2018, Antala *et al.* 2022). While anaerobic conditions enable peat accumulation and carbon storage by limiting the decomposition of organic matter, they also lead to production of CH₄, a powerful GHG with global warming potential 28 to 32 times that of CO₂ over a 100-year horizon (IPCC 2013, Etminan *et al.* 2016, Dean *et al.* 2018). In contrast, the respiration of aerobic microorganisms produces CO₂ and favours oxidation of CH₄ before it is released to the atmosphere (Moore & Dalva 1993, Lai 2009). Prolonged aerobic conditions caused by drainage lead to peat decomposition (i.e., peat mineralisation) and have several long-term effects on peat properties (reduced macro-porosity, elasticity and water storage capacity, increased compaction and consolidation, surface elevation loss, and overall homogenisation of soil properties and ecosystem functionality; Price *et al.* 2003, Gabriel *et al.* 2018, Gauthier *et al.* 2018, Howie & Hebda 2018, Liu *et al.* 2020). The recovery of peat properties to the pre-degradation state after rewetting is strongly influenced by the duration and intensity of prior drainage, which can lead to significant physical and chemical alterations of the peat. Severely disturbed and long-drained peatlands often exhibit increased bulk density, reduced porosity and decreased hydraulic conductivity, all of which impede rapid restoration. While rewetting can stabilise carbon losses and initiate recovery, natural conditions may take decades or longer to re-establish, depending on the severity of the degradation (Kreyling *et al.* 2021). Rewetting, which aims to slow down peat degradation and to restore the carbon sink function of peatlands, generally leads to a short-term (years to decades) increase in CH₄ production (Vanselow-Algan *et al.* 2015, Abdalla *et al.* 2016). However, the positive radiative effect of CH₄ emission over the short term is expected to be compensated by CO₂ sequestration over the long term (spanning several decades to centuries; Nugent *et al.* 2019, Günther *et al.* 2020, Humpeñöder *et al.* 2020, Zak & McInnes 2022).

Climate change including an associated rise in air temperature has, together with anthropogenic disturbance (e.g., drainage for agriculture, forestry, and peat extraction), led to the desiccation of temperate and tropical peatlands. This, in turn, promotes CO₂ fluxes to the atmosphere and leads to contrasting and unclear effects on CH₄ emissions (Swindles *et al.* 2019, Loisel *et al.* 2021, Kang *et al.* 2022). In addition, increased temperature and lowered WL favour the colonisation of peatlands by vascular plants, resulting in positive feedback that further amplifies the decrease in WL and the increase of CO₂ emissions (Antala *et al.* 2022).

Moreover, the complex interactions between vegetation, microorganisms, peat properties, water chemistry and WL complicate the assessment of consequences for GHG exchange between peatlands and the atmosphere (Parish *et al.* 2008, Bragazza *et al.* 2013, Waddington *et al.* 2015, Arsenault *et al.* 2019, Antala *et al.* 2022). Therefore, these global changes lead to non-linear responses in the carbon cycles of peatlands, with threshold effects (Bragazza 2008, Page & Baird 2016, Jassey *et al.* 2018, Li *et al.* 2021b, Liu *et al.* 2022).

Peatlands are also highly diversified ecosystems and thus subject to small-scale variations in WL, vegetation, microtopography and hydrophysical peat properties (Joosten & Clarke 2002, Lindsay 2010, Juszczak *et al.* 2013, Arsenault *et al.* 2019, Ahmad *et al.* 2020a, Miaorun Wang *et al.* 2021, Briones *et al.* 2022, Couwenberg *et al.* 2022). For example, microtopography causes significant variability in water depth with respect to surface vegetation, which leads to diversified microhabitats (e.g., hummocks, lawns or hollows). Microtopography also influences organic matter recycling, leading to variations in peat growth rates and GHG emissions (Chaudhary *et al.* 2018, Ming Wang *et al.* 2021, Perryman *et al.* 2022).

Beyond the internal heterogeneity of an individual peatland, considerable differences exist in peatland types and locations depending on altitude, latitude or geological framework (Joosten 2016, Wheeler & Proctor 2000). All of these heterogeneities, operating across spatial and temporal scales, influence GHG exchange with the atmosphere and must therefore be quantified to better delineate the future of peatlands regarding their ecosystem services (Limpens *et al.* 2008). Within this general scheme, temperate peatlands located at the southern distribution limit of northern peatlands (Xu *et al.* 2018) may be regarded “as ‘ecosystem sentinels’ for climate change, acting as early warning indicators of climate–carbon feedbacks” (Briones *et al.* 2022). Indeed, they may

experience temperature conditions that ecosystems farther north will not reach until later.

Temperature is a key driver for aerobic and anaerobic respiration, as well as for photosynthesis. Therefore, the increase of air temperature induced by climate change raises questions about the direct and indirect (e.g., vegetation, WL) effects of temperature on GHG exchange between peatlands and the atmosphere (Harenda *et al.* 2018, Bertrand *et al.* 2021, Li *et al.* 2021b, Antala *et al.* 2022). One approach to improving our ability to predict future fluxes is to install Open Top Chambers (OTC) which can locally induce passive warming of the air above ground (Arft *et al.* 1999, Li *et al.* 2021a). To our knowledge, few recent studies have investigated the effects of OTCs on GHG fluxes in temperate peatlands, and even fewer have been conducted in mid-altitude mountain settings (Johnson *et al.* 2013, Ward *et al.* 2013, Pearson *et al.* 2015, Lamentowicz *et al.* 2016, Oestmann *et al.* 2022, Salmon *et al.* 2022).

METHODS

Study site

The study site is located in the French Jura Mountains near the town of Frasné (840 m a.s.l., 46.826° N, 6.173° E; Figure 1A). The Frasné peatland is a large (> 300 ha) complex of different peatland types (e.g., fen, raised bog, wooded and transitional peatland). Its ecological value has been recognised by the RAMSAR convention ([RAMSAR site](#)), it is part of the European Natura 2000 network, and approximately 100 ha of the complex is also a regional nature reserve. The Forbonnet site is a transitional peatland within the complex that has been monitored since 2008. The site has belonged to the National Observatory of Peatlands ([SNO Tourbières](#); Bertrand *et al.* 2021, Gogo *et al.* 2021) since 2012 and is integrated into the French Critical Zone research infrastructure ([OZCAR](#); Gaillardet *et al.* 2018). The site also serves as an observatory for the Zone Atelier of Arc Jurassien, which is dedicated to studying the interplay between humans and nature ([ZAAJ website](#)). As a French priority research site, Forbonnet benefits from detailed spatio-temporal monitoring of meteorology and hydrology.

According to the Köppen-Geiger classification the climate of the site falls between classes Cfb and Dfb (Rubel *et al.* 2017), defining a temperate climate with contrasted seasons. Average annual air

temperature is 7 °C and monthly averages range from 0 °C (December to February) to 15 °C in July and August. Annual precipitation ranges from 1293 to 2110 mm (average ± standard deviation = 1618 ± 258 mm) and is uniformly distributed throughout the year with a mean of 135 ± 25 mm month⁻¹ (averages over the period 2009–2019; Toussaint *et al.* 2020a).

Ecologically, the Forbonnet peatland is a *Sphagnum*-dominated zone, where species such as *Andromeda polifolia*, *Vaccinium oxycoccos*, *Eriophorum vaginatum*, *Scheuchzeria palustris*, *Drosera* spp. and *Calluna vulgaris* are also observed. The peatland is surrounded by more mature and topographically higher peatlands covered with pine and spruce trees, that are progressively colonising the centre of the site. In addition, patches of *Phragmites* on the contours of the Forbonnet peatland indicate localised minerotrophic (i.e., nutrient-rich) conditions.

The Forbonnet peatland was equipped with an experimental research station in 2008 to study the effect of air temperature warming using OTC devices according to the ITEX protocol (Arft *et al.* 1999, Laggoun-Défarge *et al.* 2008). The chambers were installed along a hydrological gradient (Figures 1B–D) characterised by differences in WL (Toussaint *et al.* 2020b), microtopography and vegetation cover. The “WET” area is almost flat and homogeneous (lawn area) while the “DRY” area is characterised by more-pronounced microtopography with hummocks. The proportion of *Sphagnum* is significantly lower in the DRY than in the WET area, and reciprocally for vascular plants (Buttler *et al.* 2015). Along this hydrological gradient, which includes an intermediate location (referred to as INTER), measuring plots were distributed across the gradient with both “control” and “heated” OTC stations: DC (control) and DH (heated) in the DRY area, IC (control) and IH (heated) in the INTER area; and WC (control) and WH (heated) in the WET area.

Hydrometeorological monitoring

Air temperature was measured at each plot 10 cm above the soil surface using thermocouples (Mesurex, TT20100T). The research station is also equipped with a meteorological station recording air temperature and relative humidity (T, RH, HMP155A, Vaisala, Vantaa Finland), atmospheric pressure (278, SETRA, Boxborough MA, USA), Photosynthetic Photon Flux Density (PPFD, SKP215 Skye Ltd, Llandrindod Wells, UK), wind direction, and wind speed every 30 minutes (Windsonic Gill, Lympington,

UK; see Gogo *et al.* (2021) for more details). Due to technical issues with the automatic rain gauge during the study period, precipitation was measured monthly on site with a rain collector normalised for isotope characterisation (Palmex Rain Sampler 1C; see Lhosmot *et al.* 2022a). The WL was monitored every 30 minutes by two piezometers equipped with OTT Orpheus Mini pressure probes and installed in the WET and DRY areas along the research station boardwalk (± 0.1 %; Toussaint *et al.* 2020b).

GHG flux and auxiliary data measurements

Carbonaceous greenhouse gas (CO₂ and CH₄) fluxes between the peatland and the atmosphere were measured monthly from February 2020 to September 2021, using the non-steady state closed chamber method (Hutchinson & Livingston 1993). Fluxes were measured on six plots, constituting three pairs of control (C) and OTC (H) plots (Figure 1C). These three pairs were placed along the hydrological DRY-INTER-WET gradient (Figure 1C).

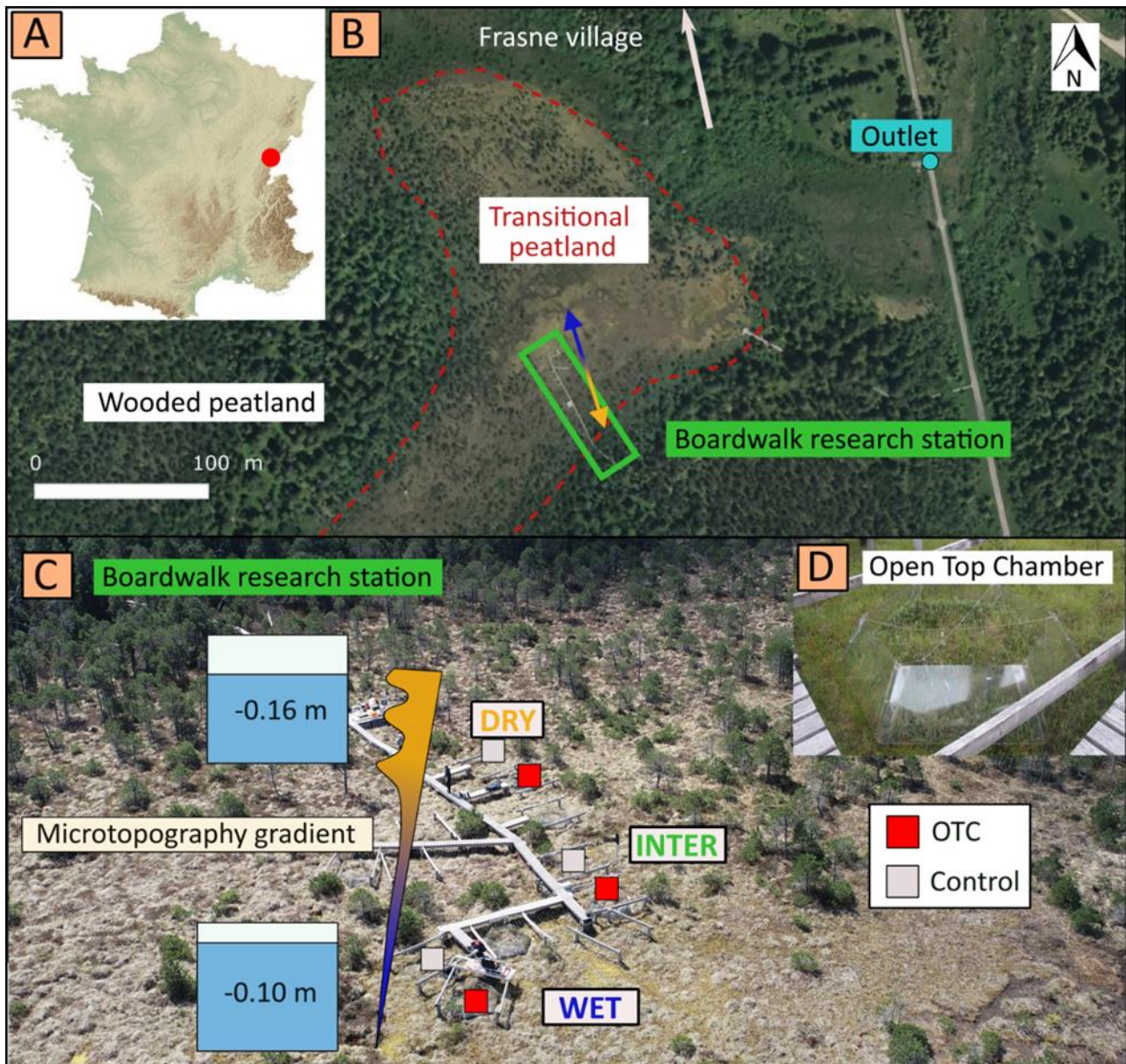


Figure 1. (A) Location of the Frasne peatland (CapCarto, 2016). (B) Location of the study plot and the boardwalk research station (IGN, 2018). (C) Location of the WET, INTER and DRY study areas (Open Lab Dream, UBFC, G. Bertrand, March 2021). The beige-blue graph next to the boardwalk is a simplified microtopographic cross-section along the WET-INTER-DRY transect. It symbolises the hummocks in the DRY area in beige and the transition towards the almost flat and wetter INTER and WET areas in blue. The median water level over the two study years (2020 and 2021) was -0.10 m and -0.16 m for the DRY and WET areas, respectively, based on 30 minute interval data. (D) Open Top Chamber.

To determine the GHG fluxes, we used a Los Gatos Research infrared laser spectrometer analyser (LGR “Greenhouse Gas Analyzer [CH₄, CO₂, H₂O] Ultraportable,” 2019), connected to a transparent plexiglass chamber (29 cm diameter and 51 cm height) in which GHG concentrations were measured for 2–4 minutes. To ensure proper homogenisation, the air inside the chamber was continuously mixed using an internal pump system. Since the chamber is translucent, the measurements represent the Net Ecosystem Exchange (NEE) of CO₂. To measure the ecosystem respiration (Reco), a second measurement was conducted using the same chamber, this time with an opaque cover. After the opaque cover was installed, measurements were considered following a stabilisation period of up to 20 seconds. The gross primary production (GPP) was then calculated as follows:

$$(NEE = Reco - GPP) \quad [1]$$

where Reco and GPP are expressed as absolute values. In this study, negative fluxes are defined as fluxes from the atmosphere to the soil, and reciprocally. Accordingly, a negative sign was assigned to GPP values. Methane measurements were similarly performed with and without the opaque cover, but no difference was observed. All flux measurements were conducted during daytime, typically between 10 a.m. and 6 p.m. Finally, the flux of GHG between the peatland and the atmosphere ($F_{(CO_2, CH_4)}$) was calculated using Equation 2 (Jacotot *et al.* 2019, Korhonen *et al.* 2019):

$$F_{(CO_2, CH_4)} = \frac{\frac{V}{S} \times \frac{dC}{dt} \times P}{R \times T} \quad [2]$$

where $F_{(CO_2, CH_4)}$ is the flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of CO₂ and CH₄ respectively, V the volume of the chamber (m^3), S the area of soil covered by the chamber (m^2), dC the difference of GHG concentration in the chamber between the start and the end of the measurement (ppm), dt the duration of the measurement (s), P the air pressure in the chamber (Pa), R the universal gas constant ($8.314 \text{ J mol}^{-1} \text{ K}^{-1}$), and T the air temperature inside the chamber (K).

During each measurement, both air temperature and pressure were measured in the chamber with a Hobo Tidbit V2 probe (accuracy $\pm 0.21 \text{ }^\circ\text{C}$) and a Baro Diver (Van Essen instruments, accuracy ± 49 Pa), respectively. In addition, the Photosynthetic Photon Flux Density (PPFD) was recorded every 30 seconds in the chamber with a light meter (ULM-500, WALZ).

Evaluation of CO₂ ecosystem respiration (Reco) sensitivity to temperature: the apparent Q_{10}

The sensitivity of ecosystem respiration to temperature variation is critical in the context of global warming. This sensitivity can be quantified using the Q_{10} parameter (Davidson *et al.* 2006), which is a temperature coefficient based on the Arrhenius (1889) law that relates variations of chemical reaction rates to temperature changes. More precisely, k , the reaction rate (s^{-1}), is related to the temperature and the activation energy by the following equation (Arrhenius 1889):

$$k = Ae^{\frac{-E_a}{RT}} \quad [3]$$

where A is the Arrhenius constant in s^{-1} with $\ln(A)$ representing the y-intercept of the Arrhenius plot ($\ln(k) = 1/T$), E_a is the activation energy required to initiate a chemical reaction in J mol^{-1} , R is the universal gas constant in $\text{J mol}^{-1} \text{ K}^{-1}$ and T is the absolute temperature (K).

The change in GHG production rates as a function of temperature variation serves as an indicator of organic matter decomposition sensitivity to temperature (Curiel Yuste *et al.* 2004, Davidson *et al.* 2006). As our study is not directly based on GHG production rates, but on GHG fluxes at the peatland–atmosphere interface, the calculated E_a and Q_{10} values correspond to apparent values (referred to as E_a and Q_{10} ; Davidson *et al.* 2006). Q_{10} is an index based on the difference in reaction rate triggered by a temperature change of $10 \text{ }^\circ\text{C}$. It can therefore be expressed as follows:

$$Q_{10} = e^{\left(\frac{E_a}{R} \left(\frac{10}{T(T+10)}\right)\right)} \quad [4]$$

E_a was calculated by the following equation after using the logarithm:

$$F_{GHG} = Ae^{\frac{-E_a}{RT}} \quad [5]$$

The air temperature measured in each plot at 10 cm above the soil surface was used to calculate Q_{10} . We showed in a previous study that methanotrophy is an important process controlling methane fluxes in the Forbonnet peatland (Lhosmot *et al.* 2022b). Hence, measured CH₄ fluxes integrate both production and oxidation of CH₄. Consequently, apparent Q_{10} is not a direct indicator of the CH₄ production alone, and we did not use Q_{10} for CH₄.

Analysis of GHG fluxes

To assess the effect of warming on GHG emissions (Reco and CH₄), we considered measurement campaigns for which OTC and control plot data were available along with all hydrological conditions (WET, INTER and DRY). Given that passive warming does not appear to be a discriminating factor (see section “Reco and CH₄ fluxes for OTC and control plots”), we finally merged the OTC and control plot data and grouped them only by hydrological conditions. This allowed a larger dataset to be used to assess the influence of WL on Reco and CH₄ fluxes. Considering the occurrence of two

contrasting hydrological conditions during the summers of 2020 and 2021 and the implementation of a high frequency GHG measurement campaign during the wet spring of 2021, we split the dataset into three seasonal conditions: (1) dry/drought summer (June–September 2020), (2) wet summer (June–September 2021), and wet spring (May 2021).

PPFD, which strongly controls GPP (Haraguchi & Yamada 2011, Leroy *et al.* 2019), showed coherent seasonal variations but high within-day variation due to cloud cover and diurnal cycles (Figure 2). Consequently, rapid variations in both PPFD and T data limited the availability of simultaneous

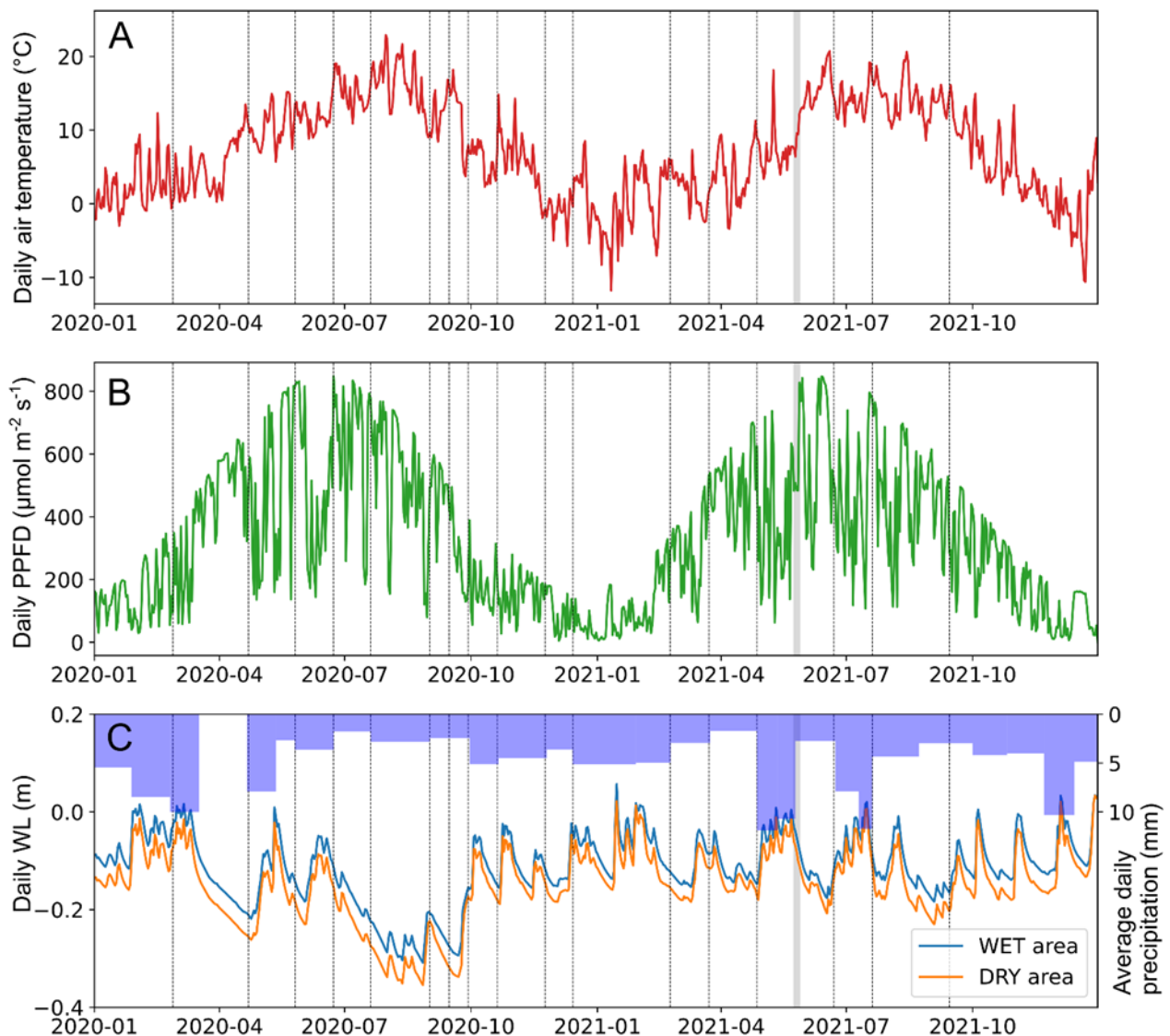


Figure 2. Daily means of hydro-meteorological data measured at the meteorological station. (A) Air Temperature. (B) Photosynthetic Photon Flux Density (PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$). (C) Water Level (WL, m) at the WET and DRY areas (left y-axis) and average daily precipitation (mm, right y-axis). The black vertical dashed line indicates the days of chamber GHG flux measurements. The grey vertical band in May 2021 indicates an intensive campaign of chamber GHG flux measurements.

measurements across the plots, thereby restricting the analysis of the relationship between GPP, air temperature and WL. To address this, the dataset was divided into two groups (DRY and WET-INTER areas) and environmental conditions favourable for photosynthetic activity (air temperature above 10 °C and PPFD between 100 and 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) were selected. This approach allowed us to identify a hydrological influence on GPP (see section “*GPP response to different hydrological conditions*”).

Statistical comparison

Statistical tests were conducted to assess differences in data distribution across similar periods for WL (between WET and DRY areas), air temperature above the soil surface (between OTC and control plots), and GHG fluxes (between OTC and control plots, as well as across different hydrological conditions [WET, INTER, DRY]). Due to the lack of normality and/or homoscedasticity in the datasets and because measurements were paired, the Wilcoxon signed-rank test was employed.

RESULTS

Hydrometeorological conditions

The study period integrated two growing seasons (2020 and 2021, Figures 2A and 2B). The daily air temperatures in the peatland were highest in summer, reaching 23 °C in July 2020, and lowest in winter, reaching -11.9 °C in January 2021, with a mean of 7.2 °C for 2020–2021 (Figure 2A). The PPFD showed a seasonal pattern similar to that for temperature, with the highest mean daily (24 hours) values in summer (848 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and values close to 0 in winter (Figure 2B). The cumulative rainfall in 2020 (from 28 Jan 2020 to 14 Dec 2020) and 2021 (from 29 Jan 2021 to 14 Dec 2021) was 1328 and 1618 mm, respectively. Reflecting precipitation, WL median in the WET area was significantly lower in 2020 (median [95 % CI]; -0.13 [-0.14, -0.11] m) compared to 2021 (-0.10 [-0.11, -0.10] m; p-value < 0.001; Figures 2C, 3A and 3B). The growing seasons (May to September) were particularly contrasting, with rainfall totalling 653 mm in 2020 and 1016 mm in 2021, resulting in a significant WL difference during this period (2020: -0.19 [-0.21, -0.17] m and 2021: -0.11 [-0.12, -0.09] m; p-value < 0.001; data from the WET area; Figure 2C). The cumulative potential evapotranspiration over May to September, calculated from daily air temperature using the formula of Oudin *et al.* (2005), was slightly higher in 2020 (472 mm) than in 2021 (449 mm). Furthermore, the WL distribution over the

two years showed significantly lower values in the DRY (-0.16 [-0.17, -0.15] m) compared to the WET area (-0.10 [-0.11, -0.10] m; p-value < 0.001; Figures 3A and 3B).

The effect of OTC on air T was evaluated across the different plots for 2020–2021 (Table S1 in the supplementary material). For all areas (DRY, INTER, WET), mean annual air T was 0.2 to 0.6 °C higher in OTC plots compared to their corresponding control plots. This temperature difference increased with PPFD (p-value < 0.001; Table S1, Figures 4A and 4B). For PPFD values above 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, OTCs increased air T from 0.6 to 1.5 °C. The temperature difference reached 1.7 to 2.0 °C for PPFD above 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Table S1). In contrast, for PPFD below 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ the temperature difference dropped to 0.2 to 0.5 °C (Figure 4A).

GHG fluxes

Seasonal variations of Reco, NEE, GPP and CH₄ fluxes

Raw flux data with associated environmental variables are available in the supplementary material (Table S2). While all fluxes were close to zero in winter, Reco reached 5.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on 23 Jun 2020, and 5.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on 14 Sep 2021. GPP reached

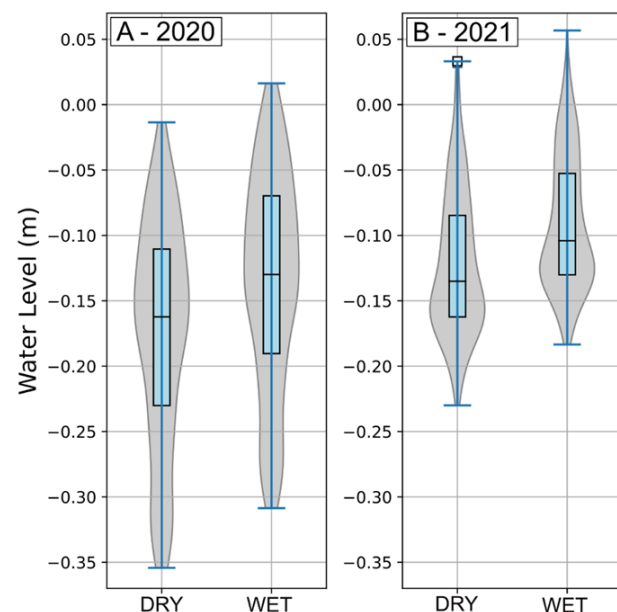


Figure 3. Violin plot showing the distribution of water level (WL) measurements for DRY and WET areas in 2020 (A) and 2021 (B), based on data for 30-minute intervals. The distribution is based on Kernel Density Estimation. The embedded boxplot indicates the interquartile range (IQR), with the median marked by a horizontal line. Whiskers extend to 1.5 times the IQR.

-9.6 and -8.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on 20 July in 2020 and 2021, respectively. NEE ranged from 3.4 to -6.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Over the two years, the highest NEE values were recorded on 20 Jul 2020 (-4.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and 20 Jul 2021 (-6.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Finally, CH_4 fluxes were mostly between 0 and 100 $\text{nmol m}^{-2} \text{s}^{-1}$, reaching 187 and 344 $\text{nmol m}^{-2} \text{s}^{-1}$ on 20 Jul 2020 and 14 Sep 2021, respectively. Flux variability between plots was close to zero in winter and fluxes increased in summer, reaching maxima of 4.6, 5.8, 8.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 326 $\text{nmol m}^{-2} \text{s}^{-1}$ for NEE, Reco, GPP and CH_4 , respectively (Figures 5A, 5B, 5C, 5D). The general trend indicates that the contrast between plots increases with increasing fluxes.

Reco and CH_4 fluxes for OTC and control plots

The statistical comparison showed no significant differences in Reco and CH_4 fluxes between the OTC and control plots along the hydrological gradient (Figures 6A and 6B; p -value > 0.05; Wilcoxon signed-rank test).

Reco and CH_4 fluxes along the hydrological gradient

Figures 7A and 7B show a statistical comparison of the Reco and CH_4 fluxes along the WET-INTER-DRY hydrological gradient, including OTC and control plots (Wilcoxon signed-rank test). For this comparison, only datasets from field campaigns where fluxes were available for all six plots were used.

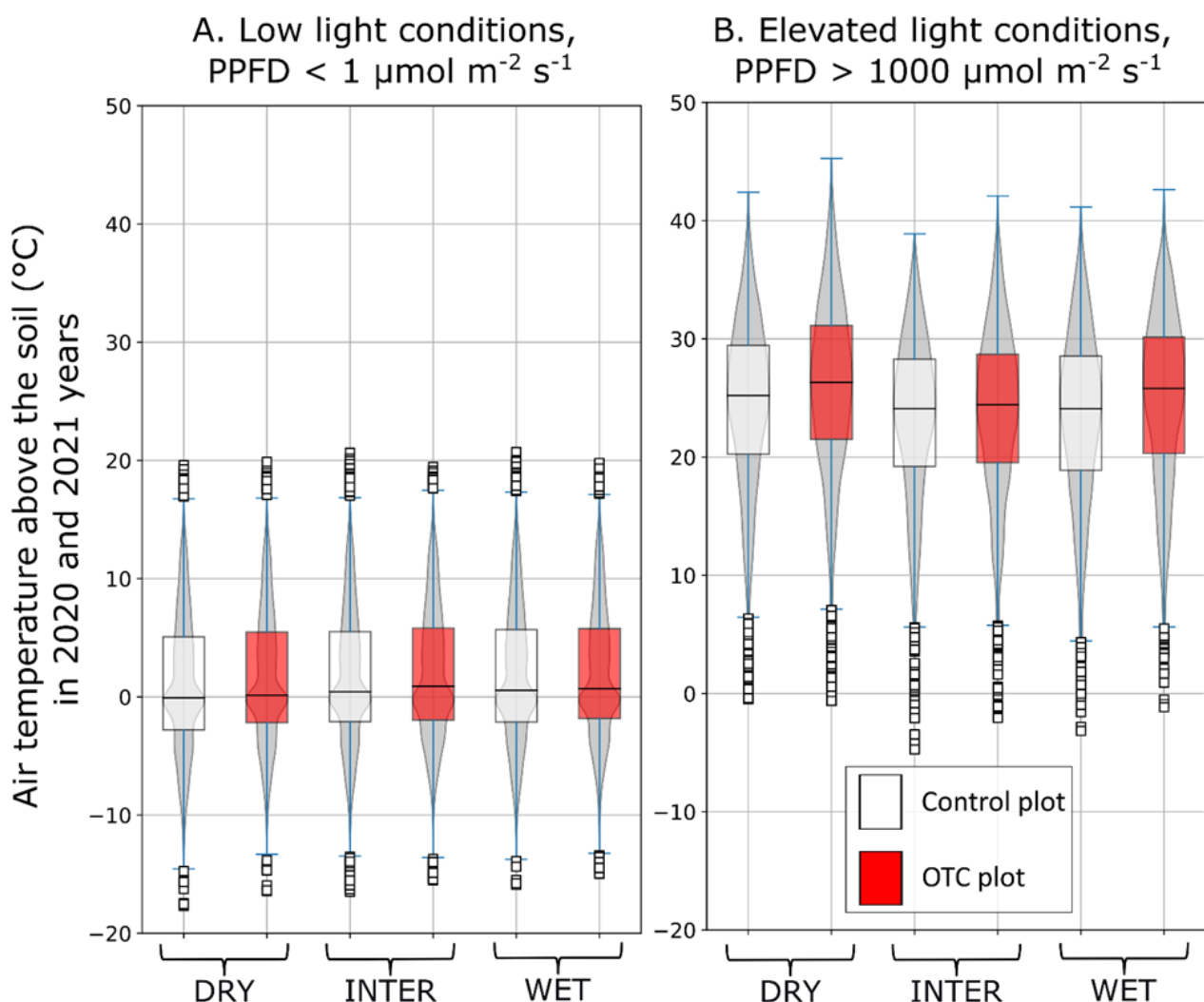


Figure 4. Violin plot showing air temperature (T , $^{\circ}\text{C}$) distribution for the six plots over the 2020–2021 period. The measurements were taken every 30 minutes at 10 cm above the soil surface. Subplots show (A) low light conditions ($\text{PPFD} < 1 \mu\text{mol m}^{-2} \text{s}^{-1}$) and (B) elevated light conditions ($\text{PPFD} > 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$), respectively. The distribution is based on Kernel Density Estimation. The embedded boxplot indicates the interquartile range (IQR), with the median marked by a horizontal line. Whiskers extend to 1.5 times the IQR.

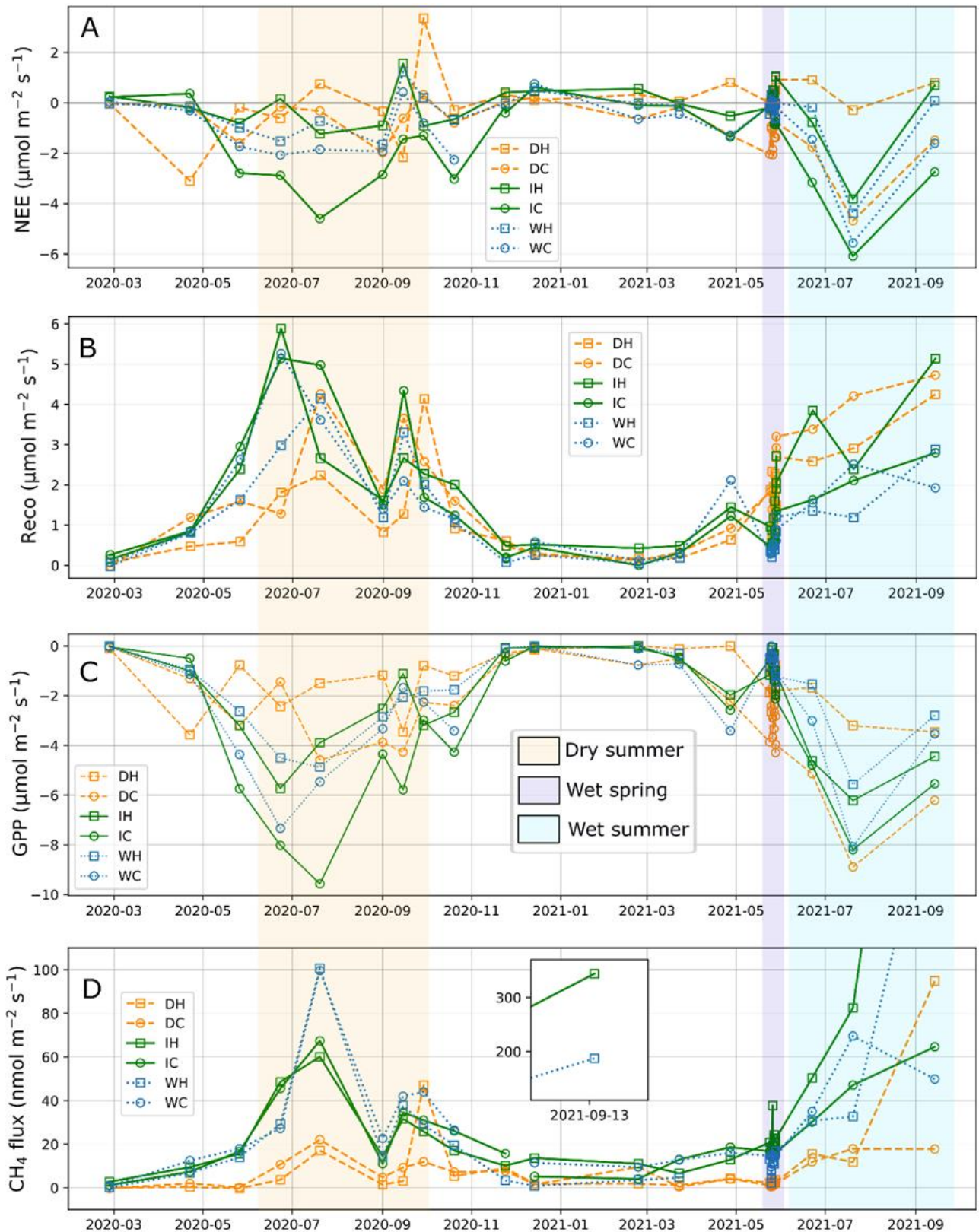


Figure 5. GHG fluxes of the individual plots. DC: control plot in the DRY area; DH: OTC plot in the DRY area; IC: control plot in the INTER area; IH: OTC plot in the INTER area; WC: control plot in the WET area; and WH: OTC plot in the WET area.

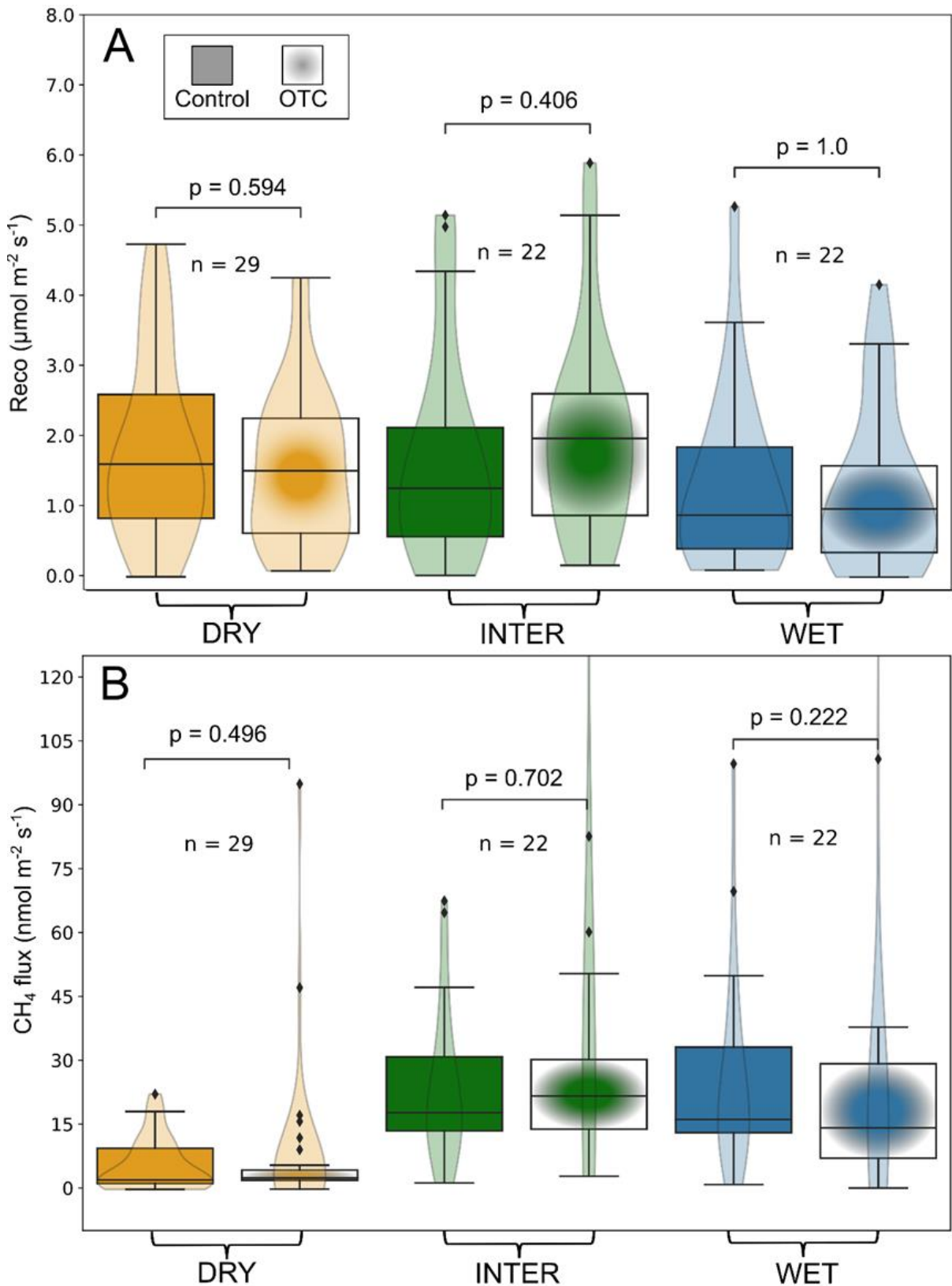


Figure 6. Violin plot showing Reco (A) and CH_4 flux (B) distribution for each study plot. The distribution is based on Kernel Density Estimation. The embedded boxplot indicates the interquartile range (IQR), with the median marked by a horizontal line. Whiskers extend to 1.5 times the IQR. The statistical comparison (p-value) between control and OTC plots was realised using the Wilcoxon signed-rank test. The y-axis of subplot B has been shortened to improve readability and to prevent the display of two extreme values (for IH, CH_4 flux = $344 \text{ nmol m}^{-2} \text{ s}^{-1}$; and for WH, CH_4 flux = $187 \text{ nmol m}^{-2} \text{ s}^{-1}$).

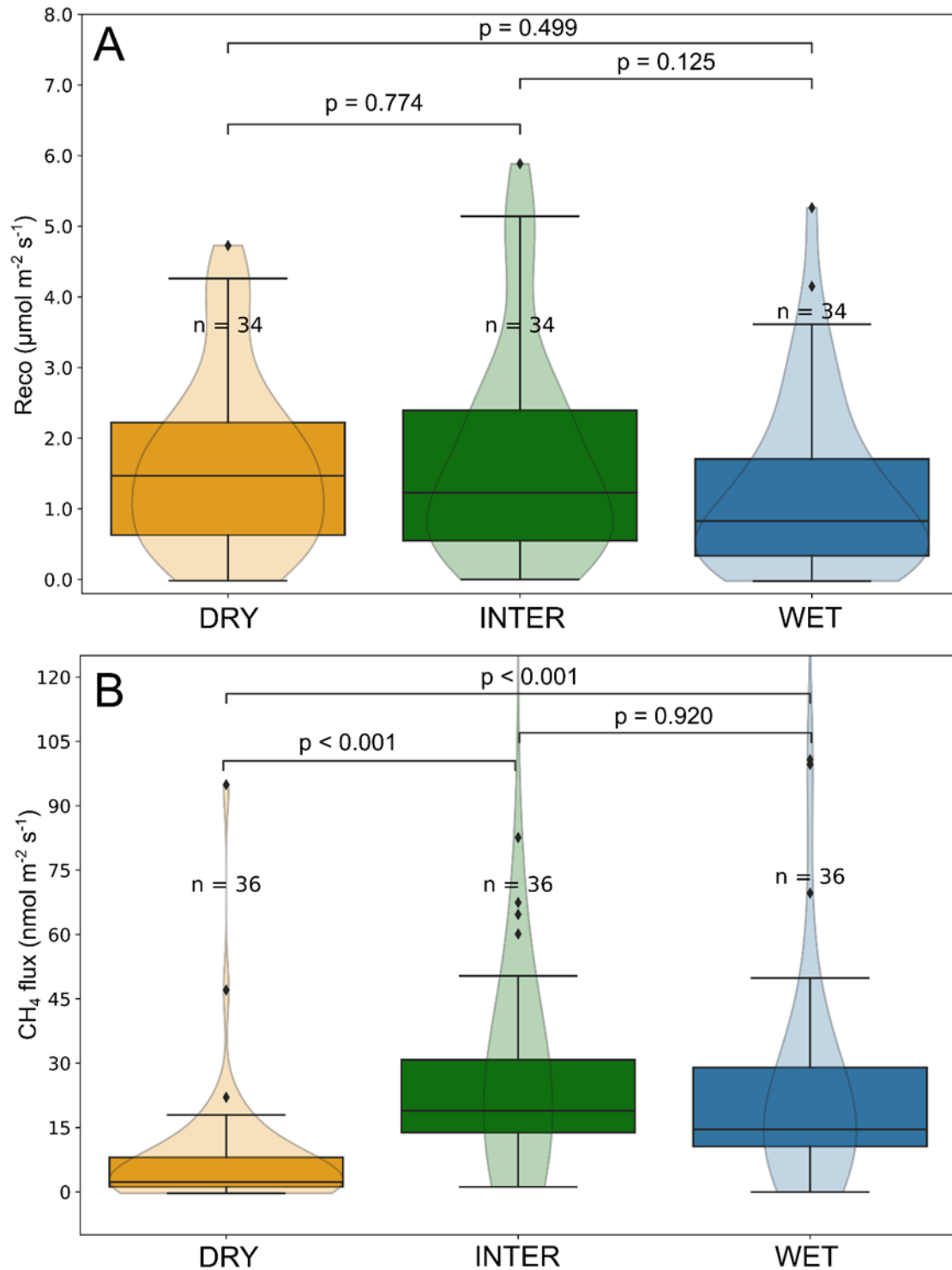


Figure 7. Violin plot showing Reco (A) and CH_4 flux (B) distribution for each hydrological condition (DRY, INTER and WET areas) including OTC and control plots. The distribution is based on Kernel Density Estimation. The embedded boxplot indicates the interquartile range (IQR), with the median marked by a horizontal line. Whiskers extend to 1.5 times the IQR. The statistical comparison (p-value) between plots of different hydrological condition was realised using the Wilcoxon signed-rank test. The y-axis of subplot B has been shortened to improve readability and to prevent the display of two extreme values (for IH, CH_4 flux = $344 \text{ nmol m}^{-2} \text{s}^{-1}$; and for WH, CH_4 flux = $187 \text{ nmol m}^{-2} \text{s}^{-1}$).

For Reco, the median flux for the DRY (median [95 % CI]; 1.7 [0.9, 2.3] $\mu\text{mol m}^{-2} \text{s}^{-1}$) and INTER (1.7 [1.0, 2.4] $\mu\text{mol m}^{-2} \text{s}^{-1}$) plots was slightly higher than for the WET area (1.2 [0.8, 1.7] $\mu\text{mol m}^{-2} \text{s}^{-1}$; Figure 7A). Regarding specific hydrological conditions (i.e., dry/drought summer [Jun–Sep 2020], wet summer [Jun–Sep 2021] and wet spring [May 2021]), the WET–DRY gradient was consistent with the gradient observed for the entire dataset in 2021 (with wet summer and wet spring conditions). For the wet summer and wet spring periods of 2021, Reco was substantially lower for the WET (1.7 [1.25, 2.75] $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 0.4 [0.3, 0.6] $\mu\text{mol m}^{-2} \text{s}^{-1}$) than for the DRY area (3.8 [2.7, 4.6] $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 1.6 [1.3, 2.0] $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively). However, during the dry summer of 2020, Reco for the DRY area (2.0 [1.3, 3.8] $\mu\text{mol m}^{-2} \text{s}^{-1}$) was slightly lower than for the INTER and WET areas (2.7 [1.7, 5.0] and 2.5 [1.4, 3.8] $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively). In addition, Reco for the DRY area was lower in the dry (2.0 [1.3, 3.8] $\mu\text{mol m}^{-2} \text{s}^{-1}$) than in the wet summer (3.8 [2.7, 4.6] $\mu\text{mol m}^{-2} \text{s}^{-1}$), while average WL was -0.27 [-0.29, -0.25] m for the dry and -0.15 [-0.17, -0.15] m

for the wet summer (June–September, DRY area, Figure 2C).

The mean CH_4 fluxes calculated from all measurements were significantly higher (p-value < 0.001) for the WET and INTER areas (17.5 [14.2, 29.0] and 20.0 [14.8, 30.4] $\text{nmol m}^{-2} \text{s}^{-1}$) compared to the DRY area (3.4 [1.9, 9.4] $\text{nmol m}^{-2} \text{s}^{-1}$, Figure 7B). In contrast, the mean CH_4 fluxes for INTER and WET areas were not significantly different (p-value = 0.92, Figure 7B). This spatial pattern was also observed at the seasonal scale.

GPP response to different hydrological conditions

In the WET-INTER areas, GPP showed a slight negative correlation with WL, with a distinct break observed at a WL of approximately -8 cm. For WL values below -8 cm GPP exhibited strong variability, ranging from 0 to -10 $\mu\text{mol m}^{-2} \text{s}^{-1}$. In contrast, for shallow WL values above -8 cm, GPP converged towards a narrow range between -2 and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 8A). No similar trend was observed for the DRY area, where GPP did not display a clear relationship with WL (Figure 8B).

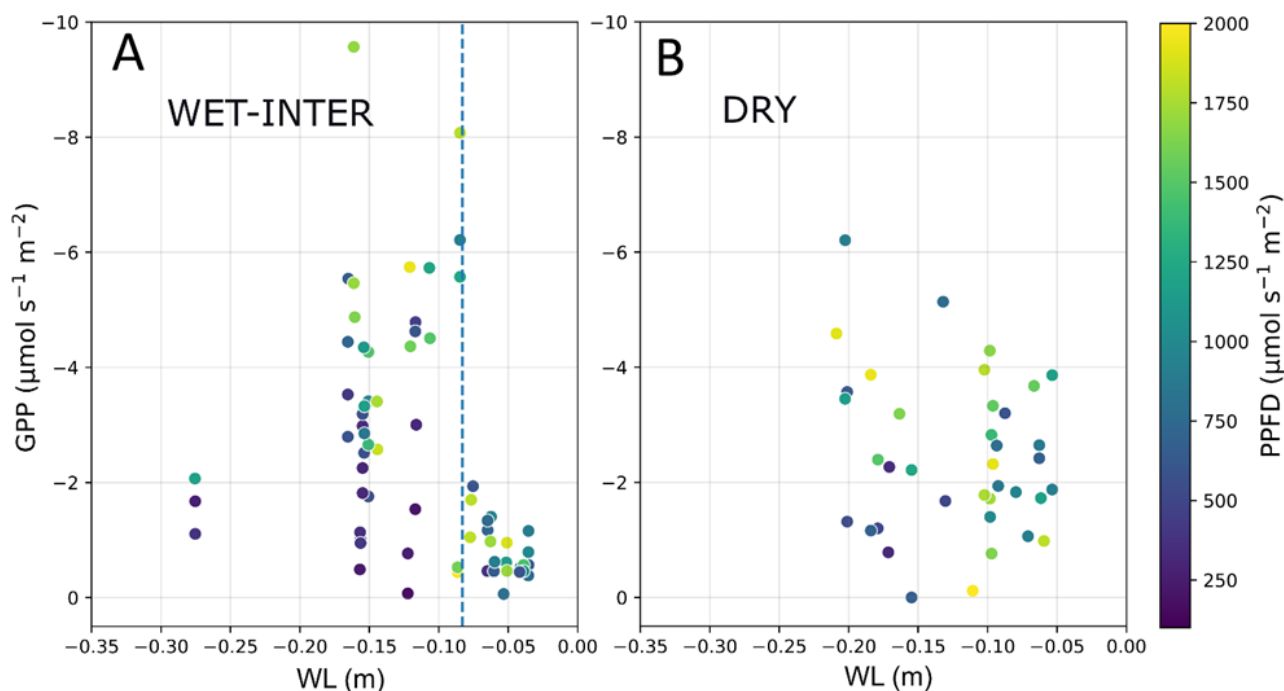


Figure 8. Correlation plot between GPP ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and WL (m) (A) in the WET and INTER areas and (B) in the DRY area. Flux data are shown only for air temperatures above 10 °C and PPFd values between 100 and 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The blue dashed line in subplot A represents the WL threshold of -0.08 m discussed in the text. The colours of the plot symbols reflect the PPFd conditions when fluxes were measured, specified by the gradient bar to the right.

Apparent temperature sensitivity of ecosystem respiration

We sorted the GHG fluxes by plot using all available data and then calculated the apparent Q_{10} and the apparent E_a for Reco (Table 1). E_a ranged from 48 to 88.6 KJ mol⁻¹ (average of 65 KJ mol⁻¹). It was slightly lower in the DRY area (~48 KJ mol⁻¹) compared to the INTER and WET areas (60.3 to 88.6 KJ mol⁻¹). No discernible difference was observed between OTC and control plots. Consequently, the Q_{10} (0–10 °C) was around 2.1 in the DRY area and achieved higher values of 2.6–4 in the INTER and WET areas (Table 1).

DISCUSSION

Northern peatlands have captured significant amounts (545–1055 Gt) of carbon from the atmosphere over the past millennia (Gorham 1991, Nichols & Peteet 2019). However, both climate and land use changes currently affect the complex functioning of these ecosystems, which in turn influences the rate of carbon exchange with the atmosphere (Loisel *et al.* 2021). Understanding the processes involved in the control of these exchanges remains a major challenge, particularly for modelling fluxes at continental scale and for their integration into global climate models (Frolking *et al.* 2009). In the present study, the flux ranges observed at Forbonnet are comparable to those measured in other temperate peatlands. For instance, Reco ranges from 0 to 5.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which is within the range reported by Samson *et al.* (2018) for northern Poland (0 to 4.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and by Lafleur *et al.* (2005) for southern Canada (< 1 to 4.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$). However, the values are lower than those observed by Juszczak *et al.* (2013) in western Poland (up to 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

Regarding GPP, the fluxes remained below -10 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in our study, which is consistent with results from other *Sphagnum*-dominated temperate peatlands (Johnson *et al.* 2013, Leroy *et al.* 2019), although higher values have also been documented (e.g., up to 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Ueyama *et al.* 2020). Similarly, our CH₄ fluxes, predominantly ranging from 0 to 100 nmol m⁻² s⁻¹, agree with other studies conducted in temperate peatlands (Leroy *et al.* 2019, Ueyama *et al.* 2020).

However, the data reported in the present study indicate that both Reco and CH₄ fluxes exhibit large variability over a distance of only 35 m (Figure 5). Identification of the drivers behind this variability represents a substantial challenge for our comprehension of GHG emissions from peatlands. The aim of the following sections is, therefore, to examine CO₂ respiration and CH₄ fluxes with respect to the two primary forcing parameters, which are air temperature and hydrological conditions.

Passive warming does not directly affect GHG emissions

The comparison of Reco and CH₄ fluxes between the OTC and control plots across the different hydrological conditions (DRY, INTER and WET) did not show significant differences (Figure 6). This outcome differs from the findings of Oestmann *et al.* (2022) and Samson *et al.* (2018), who both observed increased GHG emissions in OTC plots on temperate peatland, although the patterns were complex. Oestmann *et al.* (2022) observed increased GHG emissions, dominated by CH₄ fluxes, in OTCs on a near-natural bog in north-western Germany. Samson *et al.* (2018) observed higher Reco in OTC plots under WET and DRY conditions (due to water level manipulation) in a poor fen in northern Poland. Over the course of a two-year experiment, these authors

Table 1. Apparent E_a and Q_{10} of the Reco fluxes for the different plots.

| Hydrological gradient | Temperature control | Plot | E_a (KJ mol ⁻¹) | Q_{10} (0–10 °C) | Q_{10} (10–20 °C) |
|-----------------------|---------------------|------|-------------------------------|--------------------|---------------------|
| DRY | Control | DC | 48.0 | 2.1 | 2.0 |
| | OTC | DH | 48.3 | 2.1 | 2.0 |
| INTER | Control | IC | 88.6 | 4.0 | 3.6 |
| | OTC | IH | 60.3 | 2.6 | 2.4 |
| WET | Control | WC | 66.1 | 2.8 | 2.6 |
| | OTC | WH | 79.1 | 3.4 | 3.1 |

measured the highest Reco in plots under both DRY and OTC conditions, demonstrating that the combined effect of drying and warming is stronger than either factor alone. However, in a cold-temperate peatland in the northern USA, no contrasts in Reco and CH₄ fluxes were observed between OTC and control plots (Johnson *et al.* 2013). Similarly, Pearson *et al.* (2015) found no significant differences in Reco and CH₄ fluxes between OTC and control plots across three boreal peatlands in Finland, under a variety of hydrological conditions (pristine, short-term and long-term drainage).

The non-uniform response of GHG fluxes to OTC treatment might be explained by several factors. First, the OTC effect on soil temperature is not homogeneous. Johnson *et al.* (2013) found no difference in the seasonal average peat temperature between OTC and control plots. Regarding daily patterns, they observed that the difference in peat temperature at 5 cm depth was highly variable, depending on radiation and wind conditions. We observed that OTC increased air temperature above the soil most noticeably under high PPFD conditions (Table S1) but, using the OTC and control plots of the Forbonnet station, Delarue *et al.* (2011) found no significant temperature differences in peat below 7 cm depth. In contrast to an expected increase of soil temperature (on average 0.3 to 0.5 °C) in OTC plots, as observed by Oestmann *et al.* (2022), some studies have even showed that the surface peat temperature in OTC plots is lower due to enhanced latent heat energy loss (Dabros *et al.* 2010, Górecki *et al.* 2021). As the temperature of the peat surface is a key driver for CH₄ and Reco fluxes (Ueyama *et al.* 2020, Li *et al.* 2021b), the non-significant or possible cooling effect of OTC on peat temperature could partially explain the absence of coherent trends.

Also working at Forbonnet, Binet *et al.* (2017) showed that the OTC effect changed the fungal root symbiosis and enzyme activities of *A. polifolia* that are involved in carbon cycling and the associated Reco, albeit to varying degrees depending on the hydrological gradient. Hence, the temporal variability of sunlight and wind (Figure 2B), as well as the complexity of the OTC effect on peat temperature and microbial activity, could explain the lack of observable OTC effects on Reco and CH₄ fluxes. Given the superposition of various and complex factors controlling carbon fluxes in peatlands, the OTC effect might be overridden by other drivers. In our study the variability amongst plots of vegetation, microbial communities and peat properties introduces potential for a significant OTC effect on GHG fluxes to be obscured owing to the small number of plots, consistently with observations

elsewhere (Juszczak *et al.* 2013, Ward *et al.* 2013). For instance, Ward *et al.* (2013) observed that CH₄ emissions were more strongly controlled by vegetation composition than by warming in a temperate blanket bog in northern England.

Hydrological contrasts affect GHG emissions depending on the season

CO₂ ecosystem respiration (Reco)

The higher Reco measured in the DRY area aligns with expectations. The drier conditions, coupled with a higher proportion of vascular plants and their associated litter, favour aerobic decomposition of organic matter, thereby increasing Reco (Limpens *et al.* 2008, Leroy *et al.* 2017, Li *et al.* 2021b). The evaluation of the apparent sensitivity of Reco (Q_{10} , E_a) to temperature variations highlighted consistent differences between the WET-INTER (Q_{10} between 2.6 and 4) and DRY areas ($Q_{10} = 2.1$; Table 1). The difference in Q_{10} values is even more significant than the absolute value of Q_{10} itself. The temperature range over which Q_{10} is calculated (i.e., Q_{10} for temperature variation between 0 and 10 °C) and the specific temperature utilised (i.e., air or different soil depths) can change the absolute value of Q_{10} (Samson *et al.* 2018, Helbig *et al.* 2019). The variability of Q_{10} observed at Forbonnet may reflect variations between the WET-INTER and DRY areas in terms of the lability of organic matter, which is a determining factor triggering CO₂ production from organic carbon decomposition (Conant *et al.* 2008). This hypothesis is consistent with observations from Leroy *et al.* (2017), who conducted a mesocosm experiment with peat cores from a temperate peatland. These authors observed higher sensitivity of Reco to temperature in plots dominated by *Sphagnum* ($Q_{10} = 3.75$, $E_a = 92.2$ KJ mol⁻¹) compared to plots with vascular plants (*Molinia*, $Q_{10} = 2.58$, $E_a = 65.7$ KJ mol⁻¹) that were suspected to release exudates of labile organic compounds. Consistent with our findings, Samson *et al.* (2018), found higher Q_{10} for wetter (from 2.9 to 6.1) than for drier areas (2 to 4) in a temperate peatland. However, this is the opposite of what is generally observed in peatlands, i.e., an increase in Q_{10} under drier conditions (Liu *et al.* 2024). This contrast suggests that, in the studies of Samson *et al.* (2018) and ourselves, higher temperatures were generally associated with lower water level and thus drier conditions. According to Samson *et al.* (2018), the higher Q_{10} in the wettest area indicated “a high reactivity of respiration rate when the organic matter got exposed to aerobic conditions”.

Interestingly, the higher Reco observed in the DRY area did not persist during the dry summer

period of 2020. Although the difference was not significant, it may indicate a threshold at which Reco slows down. While it is commonly accepted that Reco increases with WL drawdown, the underlying processes are complex and non-linear. For instance, Jassey *et al.* (2018) showed, in a peatland in northern Poland, that the increase in Reco only became significant at WL below -25 cm. In contrast, Liu *et al.* (2022) found in a mountainous peatland in China that Reco increased with WL drawdown until a value of -30 cm was reached, beyond which the flux no longer changed with WL depth. Other studies concluded that the heterotrophic respiration of microorganisms and the related activity of phenol-oxidase enzymes may be drastically reduced during intense droughts (Criquet *et al.* 2000, Kang *et al.* 2022). This mechanism may explain why Reco was lower in the DRY area during 2020, when WL dropped below -30 cm (Figure 2C).

CH₄ fluxes

Higher CH₄ fluxes for the WET and INTER areas strongly suggest a hydrological control over these fluxes. The reduced thickness of the aerobic peat layer due to the near-surface WL in these environments might limit oxidation and simultaneously favour CH₄ production by the thicker anaerobic compartment. Consistently, a positive relationship between CH₄ emissions and WL has been observed in numerous studies (Moore & Knowles 1989, Turetsky *et al.* 2014, Abdalla *et al.* 2016). In addition, our results align with those of Johnson *et al.* (2013), who observed lower CH₄ emissions in the driest hydrological environment (hummocks) of a cold-temperate peatland.

The hydrological WET-INTER-DRY gradient promoted non-gradual significant differences in CH₄ fluxes. Indeed, there was a marked change at the DRY-INTER transition, suggesting rapid lateral shifts in the biogeochemical behaviour of the peatland at the metre scale. Additional factors beyond WL may have contributed to this rapid spatial change of CH₄ fluxes. One of these could be the WL-controlled spatial variation of vegetation between the DRY and WET-INTER areas. This botanical contrast, characterised by denser vascular plant coverage in the DRY area, could have led to changes in plant litter and microbial communities, both of which play key roles in organic matter recycling (Trinder *et al.* 2008, Jassey *et al.* 2011a,b, Andersen *et al.* 2013). For instance, Strakova *et al.* (2011) showed that vegetation type and its associated litter influence microbial activity more strongly than decreasing WL. While the flat terrain in our experimental transect suggested gradual WL changes,

it is likely that the pronounced microtopography in the DRY area accentuated the WL difference compared to the INTER and WET areas.

Effect of water level on GPP

While the variability of GPP reflected the seasonality of PPFD intensity and of plant phenological stages (Figures 2A and 2B), our data also show faster fluctuations superimposed on this seasonality (Figure 5C). The seasonal dynamics of plant phenology and differences in vegetation cover between plots, as well as hydrological and passive warming effects, provide a potential explanation of this short-term and inter-plot variability in GPP (Tuittila *et al.* 2004, Korrensalo *et al.* 2017, Walker *et al.* 2017, Järveoja *et al.* 2018, Peichl *et al.* 2018). GPP responds rapidly to changes in PPFD (e.g., diurnal cycle, fluctuations in cloud cover; Chojnicki *et al.* 2010) because the photosynthetic rate increases with PPFD until it reaches a saturation point which depends on plant species (Haraguchi & Yamada 2011, Leroy *et al.* 2019). In our experiment, the variability of PPFD complicated the analysis of the forcing factors influencing GPP, which is an essential component of the net ecosystem carbon balance (Chapin *et al.* 2006). A more extensive dataset, including many GPP values across a wide range of PPFD fluxes under different conditions and seasons (e.g., by using different light filters on the chambers) would be necessary to disentangle the forcing effects on GPP. Nevertheless, our results show a clear influence of hydrological conditions on GPP (Figures 8A and 8B). The abrupt drop in GPP in the WET and INTER areas at WL above -8 cm could be attributed to the immersion of *Sphagnum* mosses, which significantly limited GPP due to the lower diffusion of CO₂ in water compared to air (Williams & Flanagan 1996). Field observations indicated that *Sphagnum* mosses in the WET and INTER areas are indeed partially immersed when WL exceeded -8 cm. This result aligns with Tuittila *et al.* (2004), who observed the photosynthetic response of *Sphagnum* in a restored peatland. They reported a unimodal response curve with a WL optimum of -12 cm and a significant decrease below -22 cm and above 1 cm.

These findings support the observation that GPP decreases significantly in peatlands in response to extreme hydrological conditions (Ratcliffe *et al.* 2019). While low WL can also inhibit photosynthetic activity, this was not observed in our study (Williams & Flanagan 1996). Ahmad *et al.* (2020b), however, provided evidence that rewetting improves the hydrological buffering capacity, reducing the water level fluctuations in response to precipitation events. In pristine and restored peatlands, an upper elastic peat

layer is often present, albeit not always and with spatial variability (Morris *et al.* 2011, Baird *et al.* 2016). This layer enables a hydrological self-regulating mechanism known as “bog breathing”, which stabilises WL relative to vegetation (Howie & Hebda 2018, Morton & Heinemeyer 2019). However, in northern temperate latitudes, climate change exacerbates hydrological extremes such as droughts and heavy precipitation events. This intensification may increase WL variability, pushing extremes beyond the buffering capacity of bog breathing (Spinoni *et al.* 2018, Bertrand *et al.* 2021). These contrasting forces on WL variability raise significant uncertainties regarding the future of GPP values in peatlands.

Concluding perspectives

This study investigated the spatio-temporal variability of GHG emissions in the peatland of Forbonnet at Frasné, a long-term observatory of a mid-altitude mountain peatland. This site allows the study of GHG fluxes and associated hydrometeorological and ecological conditions at various timescales. Our study documents the added value of such an observatory, especially when combined with additional point measurements to highlight the spatial variability of GHG fluxes. Our analysis of monthly chamber flux data over 20 months revealed several key findings: (1) the Open Top Chamber (OTC), which warms the air above the soil surface, had no measurable effect on CO₂ and CH₄ fluxes. Instead, we found (2) that CO₂ and CH₄ fluxes evolved along a 35 m transect with a natural hydrological gradient from WET area with a near-surface water level to DRY area with a lower water level. However, replicating this kind of study with a larger number of plots and at higher temporal resolution, especially during periods with strongly contrasting air and soil temperatures between OTC and control plots, could potentially clarify the effects of OTC on GHG fluxes.

Our results confirm the well-established hydric control on CO₂ and CH₄ emissions (Reco and CH₄ fluxes). However, we found that this control is non-linear, raising questions about the future effects of climate change. Projections predict increasingly extreme weather conditions for the study area, with wetter and warmer winters on the one hand and drier and hotter summers on the other (Bertrand *et al.* 2021), which will have implications for GHG emissions from peatlands. However, in the driest area during summer drought conditions, our data did not confirm the expected higher CO₂ ecosystem respiration. We attribute this observation to a threshold effect during droughts that limits the aerobic decomposition of organic matter.

The contrasting responses of Reco to hydrological conditions highlight the complexity of mechanisms and feedback loops involved in organic matter recycling under aerobic conditions and the associated CO₂ emissions (Gilbert *et al.* 1998, Andersen *et al.* 2013, Binet *et al.* 2017, Jassey *et al.* 2018). As a result, a more comprehensive dataset is needed to further explore the above mechanisms, especially during droughts combined (or not) with heatwaves, which are becoming more frequent and more severe in temperate latitudes (Samaniego *et al.* 2018, Spinoni *et al.* 2018, IPCC 2022). The non-linear response of Reco to WL variations raises questions about its effect on NEE, provided that GPP is also limited under more extreme conditions (Tuittila *et al.* 2004).

CH₄ emissions from peatlands are known to increase with wetter conditions, a behaviour observed in the present study at the scale of a few metres. Nonetheless, the non-progressive transition between low- and high-emission areas suggests that WL is not the sole controlling factor. Other factors such as peat materials and/or microbial communities (methanogens and methanotrophs) may also play a role in modulating CH₄ emissions. Studies including the characterisation of both microbial communities and GHG exchanges with the atmosphere should aid in improving our understanding of the processes that govern these fluxes.

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AUTHOR CONTRIBUTIONS

AL wrote the original draft. AL, GB, AJ and PB participated in conception of the study, designed the methodology and analysed the data. AL, GB, PB, MLT, RC and AB participated to the GHG field measurements. MLT acquired soil-meteorological data. Supervision and funding management of the study: GB. All authors contributed to writing, and approved the definitive version of the manuscript.

DATA AVAILABILITY

Chamber GHG fluxes measured in this study are available in supplementary data files. Meteorological and water level data are available on the Zenodo repository <https://zenodo.org/record/3763342> and <https://zenodo.org/record/3763766>. Complementary data on the Forbonnet hydrology and eddy covariance measurements are available at <https://onlinelibrary.wiley.com/doi/10.1002/eco.2315>, <https://onlinelibrary.wiley.com/doi/10.1002/hyp.14781> and <https://link.springer.com/10.1007/s10021-022-00809-x>.

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