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Abstract. Peatlands are a highly effective natural carbon sink. However, the future of the carbon stored in these ecosystems is still uncertain because of the pressure they undergo. As estimation of the peatland carbon balance shows whether the system functions as carbon sink or source. La Guette peatland is a temperate *Sphagnum*-dominated peatland invaded by vascular plants, mainly *Molinia caerulea.* The studied site was hydrologically disturbed for years by a road crossing its southern part and draining water out of the system. Our aim was to estimate the main carbon fluxes and to calculate the carbon balance at the ecosystem scale. To reach this goal, CO_2 and CH_4 fluxes, DOC content as well as environmental variables were measured monthly for 2 years on 20 plots spread across the site to taking into account spatial variability. The peatland carbon balance was estimated using empirical models. Results showed that the CO_2 fluxes were above 1000 gC m^{-2} yr^{-1}. In 2013 and 2014 the peatland was a net C source to the atmosphere with an emission of 220±33 gC m^{-2} yr^{-1}. These results provided evidence that restoration should be performed in order to reduce the water losses and favour the *Sphagnum*-dominance of this peatland.

Keywords: CO_2; CH_4; DOC; peatland; ecosystem respiration; gross primary production

1 Introduction

Peatlands are vegetated wetlands that can act as a powerful natural Carbon (C) sink. While they cover only 3% of the emerged lands (Lappalainen, 1996), the C stored in their soils has been estimated to range from 473 to 621 GtC (Yu *et al*, 2010), which represents more than 30% of the C stored in terrestrial soils, estimated between 1500 to 2400 PgC (Ciais *et al*, 2013). Thus, peatlands are of a great importance in the actual context of global changes and their preservation is essential to prevent the C stored in soil to be released to the atmosphere. However, peatlands are mostly located at high latitudes of the northern hemisphere (Strack, 2008) where the greatest climate changes are predicted to occur by the IPCC models (Christensen *et al*, 2013). Under these modified climatic conditions, the behaviour of peatlands in terms of C cycle is still uncertain.

Actually, the C balance in peatlands covers a wide range of C functioning, from sink to source (Beyer and Höper, 2015; Carroll and Crill, 1997; Koehler *et al*, 2011; Vanselow-Algan *et al*, 2015). However, the majority of these estimations were calculated on high latitudes sites, mostly in Northern Europe or in Canada where the winter is cold (Peichl *et al*, 2014; Strack and Zuback, 2013; Trudeau *et al*, 2014; Waddington and Roulet, 2000), even if few studies have been conducted in lower latitudes (below 50°) where warmer climatic conditions prevail (*e.g.* Bortoluzzi *et al*, 2006).

In addition to climatic pressure, peatlands can be submitted to anthropic disturbances, and temperate peatlands have been widely transformed by the past into agricultural or forestry lands (Joosten and Clarke, 2002). Drainage that leads to major hydrological disruption is usually a prerequisite before peatland exploitation (Beyer *et al*, 2015). For example, lowering the water table level can change the equilibrium between CO_2 and CH_4 emissions and thus modify the C balance of the ecosystem (Chimner et al, 2017). Indeed, increasing the thickness of the oxic layer can lead to (i) higher CO_2 fluxes to the atmosphere due to faster decomposition rates of soil organic matter and (ii) lower CH_4 fluxes due to the decrease in CH_4 production and/or increase in CH_4 oxidation during its transport to the surface of the soil (Lund *et al*, 2012; Pelletier *et al*, 2007). As a result of both drainage and climatic change, most temperate peatlands are now invaded by vascular plants (Berendse *et al*, 2001; Buttler *et al*, 2015).

Invasive vegetation can play a major role in CO_2 and CH_4 emissions by (i) producing litter that is more easily degradable than mosses, (ii) altering the growth of subservient species such as *Sphagnum* mosses, and/or (iii) allowing more CH_4 to be transferred to the atmosphere through the plant aerenchyma (Bubier *et al*, 2007; Francez and Vasander, 1995; Gogo *et al,* 2011; Armstrong et al., 2015). The role of the vegetation on the C fluxes are often related to a comparison between different plant community composition (Ward et al., 2013; Noyce et al., 2014); however only a few of them have attempted to integrate vegetation directly in a C balance model (Bortoluzzi *et al,* 2006; Kandel et al., 2013; Leroy et al., 2019).

In this context, the aim of this study was to investigate what is the C-sink function of a disturbed temperate peatland and the mechanisms controlling it. Here, CO_2 fluxes and CH_4 emissions were monthly measured on twenty points distributed homogeneously over a temperate peatland recently invaded by a graminoid plants, *Molinia caerulea.* Then C fluxes measurements were related to biotic and abiotic factors to estimate the annual C budget by using CO_2 and CH_4 models including, or not, vegetation index. Thus, the hypotheses tested were:

(i) the drainage and the invasion by vascular plants promoted the C emissions and lead the peatland to act as a C source

(ii) the use of vegetation index into models leads to a better representation of fluxes

2. Materials and methods

2.1 Description of the La Guette peatland

The study was performed in La Guette peatland, a *Sphagnum* peatland located in France (Neuvy-sur-Barangeon, Cher, N 47°1944, E 2°1704; Fig. 1). It is a transitional poor fen (with a pH between 4 and 5 and a conductivity lower than 80 µS m^{-2}) with a maximum peat thickness of about 180 cm. Mean annual temperature was 11°C and mean annual rainfall 732 mm for the period 1971–2000 (Gogo et al., 2011). The site is drained in its south part by a road built before 1945 that crosses the peatland. In 2009 the drainage ditch of the road was scraped, lowering the output level and consequently increasing the water losses. This hydrological disturbance in addition to a fire (in 1970's) has probably contributed to the invasion of the site by vascular plants, mainly *Pinus sylvestris*, *Betula* spp. (*Betula verrucosa* and *pubescens*) and *Molinia caerulea*; This *Poaceae* is now invading numerous peatlands in Europe mainly, due to an increase of the nitrogen deposition and drainage (Chambers et al., 1999) and thus at the detriment of the specific peatland species composed of *Sphagnum cuspidatum* and *Sphagnum rubellum*, *Eriophorum augustifolium*, *Erica tetralix* and *Calluna vulgaris.* .

2.2 Carbon fluxes measurements and calculation

In June 2011, 20 stations were set up on the peatland by dividing the area in twenty squares with a grid and choosing randomly one plot (2 m²) within each square (stratified random sampling). This method allowed a homogeneous spatial covering of the studied site (Fig. 1). Fluxes were monthly measured between March 2013 and February 2015 using a semi-cylindrical transparent static chamber equipped (30 cm of diameter, 30 cm height). The chamber was equipped with a HMP 75 sensor (Vaisala Oyj, Vantaa, Finland) to record the temperature and air humidity variations within the chamber during the incubations. In addition, a small fan allowed the air to be homogenized within the chamber (Pumpanen *et al*, 2004). CO_2 fluxes were measured in each of the 20 stations during twenty field campaigns thanks to a CO_2 sensor (GMP 343 model, Vaisala Oyj, Vantaa, Finland) placed inside the chamber. Fluxes were measured at light for Net Ecosystem Exchange (NEE) and with the chamber covered with a light insulating fabric to simulate night conditions and measure the Ecosystem Respiration (ER). Each measurement lasted between 3 to 5 minutes, and the CO_2 concentration inside the chamber was recorded at 5Hz. CH_4 fluxes were measured thanks to the SPIRIT instrument, an Infrared Spectrometer developed by the Laboratory of Physics and Chemistry of Environment and Space, (LPC2E, Orléans, France, Guimbaud *et al*, 2016, 2011; Robert, 2007). For logistical reasons (weight and long start-up time of SPIRIT), CH_4 measurements were only performed during 12 field campaigns and on only 5 stations. These measurements regularly required to access to the plots, so, wooden planks was used as mobile pontoons to limits disturbances

CO_2 and CH_4 fluxes were then calculated as follow:

$$F = \frac{dX}{dt} * \frac{P}{R*T} * \frac{V}{S} \qquad (1)$$

With F the net gas flux (µmol m^{-2} s^{-1}); dX/dt the gas concentration (µmol mol^{-1}) variation during the incubation time (s); P the atmospheric pressure (Pa); R the ideal gas constant (8.3144621 J mol^{-1} K^{-1}); T the average temperature (K) within the chamber during the incubation; V the total volume of the system (m^3); and S the chamber surface (0.283 m^2). For CO_2 fluxes, F corresponds to NEE when measured in light, and to ER when measured in the dark.

In addition with gas fluxes, dissolved organic carbon (DOC) flux was estimated monthly during the studied period. Water was sampled at the peatland outlet, filtered at 0.45 µm and *in-situ* acidified with 2 drops of H_3PO_4. The DOC concentration was then determined in the laboratory thank to a TOC-LCPH analyser (Shimadzu, Kyoto, Japan).

2.2 Monitoring of environmental variables and vegetation cover

Soil-meteorological variables were automatically monitored at a 30-min frequency during the entire studied period thanks to an automatic station installed on the site in November 2010 (Fig. 1). Parameters recorded were the total rainfall, net solar radiation, atmospheric pressure, wind direction and speed, air temperature, relative humidity and soil temperature at -5,-10, -20, and -40 cm depths. In addition, four automatic piezometer spread into the peatland allowed to record the Water Table Level (WTL) variations at the ecosystem scale (Binet *et al*, 2013). In addition to automatic measurements, manual recording of WTL, Photosynthetically Active Radiation (PAR), soil temperatures (-5, -10, -15, -20, -25, -30, -40, -50, -60, -70, -80, -90, -100 cm depth) and atmospheric pressure were realized at each measurement campaign.

A vegetation Index (VI) was calculated (Eq. 2) by summing the percentage of vegetation cover in each soil collar following three distinct plant strata: the muscular (*Sphagnum* spp.), herbaceous (*Molinia caerulea* and *Eriophorum augustifolium*), and shrub (*Erica tetralix* and *Calluna vulgaris*) strata divided by the total potential cover TC (TC = n x 100, n being the number of vegetation strata recorded):

$$IV = \frac{MS+HS+SS}{TC} \qquad (2)$$

With MS, HS and SS the percentages of cover of the muscular, herbaceous and shrub strata, and TC the sum of percentages of the three strata.

2.3 Modelling of high-frequency ER, GPP, F_{CH_4} and DOC

The C balance estimation was conducted in 3 successive steps: i) calibration to establish the relationship between gas fluxes and environmental variables; ii) evaluation to determine the relevance of these relationships in a broader context; and iii) interpolation to integrate these relationships over time and to calculate a Net Ecosystem Carbon Balance (Chapin et al, 2006):

$$NECB=GPP-ER-F_{CH4}-F_{DOC}-F_{DIC}-F_{PC}-F_{VOC}-F_{CO} \quad (3)$$

with GPP (Gross Primary Production), F_{CH4}, F_{DOC}, F_{DIC}, F_{PC}, F_{COV}, F_{CO}, the fluxes of CH_4, Dissolved Organic Carbon (DOC), Dissolved Inorganic Carbon (DIC), Particulate Carbon (PC), Volatile Organic Carbon (VOC) and Carbon Monoxide (CO), respectively. In terms of quantity, the first 4 terms are the most abundant and were estimated in the present study to calculate the C budget. By convention the negative sign refers to carbon lost by the ecosystem.

The available data were averaged by field campaign to reduce the spatial variability of the fluxes and then used to produce a high-frequency (1-hour) dataset. For this, the relationship between gas fluxes and environmental variables was fitted using non-linear regression curves. Robustness of adding a variable to the models was evaluated following three comparative criteria. First, the adjusted R^2 (R^2_a; Eq. 4) were used to estimate the proportion of explained variance:

$$R_a^2 = 1 - \left(1 - (1 - \frac{\sum(y-\hat{y})^2}{\sum(y-\bar{y})^2})\right) * \frac{n-1}{n-p-1} \quad (4)$$

with R^2 the traditional R^2, y the measured data, ŷ the modelled data, n the number of observations and p the number of predictors.

Then, the Normalized Root Mean Square Error (NRMSE; Eq. 5) was applied to evaluate the differences between measured and modelled data points respectively:

$$NRMSE = 100 * \frac{\sqrt{\left(\frac{\sum(y-\hat{y})}{n}\right)}}{\bar{y}} \quad (5)$$

with y the average of the measured data.

Finally, the relevance of adding a new variable in the model was estimated by the Akaike Information Criterion (AIC; Eq. 6; Akaike, 1974; Burnham and Anderson, 2002).

$$AIC = -2 \times log(L) + 2 \times p \qquad (6)$$

with L the maximum likelihood.

The NEE, ER, and CH_4 fluxes were modelled separately and the annual carbon balance was calculated as the sum of the model interpolations at a 1h time step. This interpolation was done made using (i) the high frequency measurement values for temperature and (ii) a linear interpolation between the punctual measurements for vegetation. For all gaseous fluxes two models are presented: one using temperature as this model is widely used (Ballantyne et al, 2014) and, the other being the best model estimation using vegetation (Bortoluzzi et al, 2006; Kandel et al, 2013). Evaluation of models 1 and 2 for GPP, ER and FCH_4 was realized using an independent dataset that includes CO_2 and CH_4 fluxes conducted in the same peatland in 2014 and using similar techniques as in the present study (unpublished data).

For GPP, the saturated GPP (GPP_{sat}) was first calculated following June *et al.* (2004) (Eq. 7), and secondly by a modified version of the equation that incorporates the vegetation index (Eq. 8):

$$GPP_{sat}\text{-1} = a * e^{\left(\frac{T-b}{c}\right)^2} \qquad (7)$$

$$GPP_{sat}\text{-2} = (a*VI+d) * e^{\left(\frac{T-b}{c}\right)^2} \qquad (8)$$

Then, GPP-1 and GPP-2 were calculated using Eq. 9 proposed by Bubier *et al.* (1995) and reused in many studies (e.g. Bortoluzzi *et al*, 2006; Worrall *et al*, 2009):

$$GPP = \frac{GPP_{sat} * i * PAR}{GPP_{sat} + i * PAR} \qquad (9)$$

with a the rate of electron transport at light saturation (µmol m^{-2} s^{-1}), b the optimal temperature for a (°C), and c the difference in temperature from b at which GPP_{sat} equals to e^{-1} of its value at b (June *et al*, 2004), T the air temperature (°C), and VI the vegetation index.

Concerning ER, the equation proposed by Luo et Zhou (2006) was used for ER-1 and modified with the integration of the herbaceous strata (HS) for ER-2:

$$ER\text{-1} = a * e^{(b*T)} \qquad (10)$$

$$ER\text{-}2 = (a*HS+c)*e^{(b*T)} \quad (11)$$

with T the air temperature (°C); a, b and c the fitted parameters and HS the cover of the herbaceous strata (%).

Finally, modelled NEE have been calculated from GPP and ER as NEE = GPP – RE. Negative values of NEE correspond to an emission of carbon from the ecosystem to the atmosphere and positive values to a fixation of carbon.

The two models of CH_4 fluxes were estimated following:

$$F_{CH4}\text{-}1 = a*e^{(b*T)} \quad (12)$$

$$F_{CH4}\text{-}2 = a*e^{(b*VI)} \quad (13)$$

with T the air temperature (°C); a and b the fitted parameters and IV the vegetation index.

High frequency of DOC fluxes (F_{DOC}) have been extrapolated using the monthly measured concentrations of DOC and an estimation of the water quantities leaving the ecosystem (D) using a hydrological model specifically calibrated for the La Guette peatland (Binet *et al,* 2013):

$$F_{DOC} = D*[DOC] \quad (14)$$

2.5 Spatial variability of CO_2 fluxes

To estimate the spatial variability of the CO_2 fluxes, the best models were also calibrated for each of the 20 plots individually. Hence the model parameters R^2a and NRMSE were estimated for each measurement point as well as the annual CO_2 flux.

3. Results

3.1 Environmental monitoring

Variations of air temperature, rainfall, and water table level are presented in Fig. 2. Between 2011 and 2015 the mean annual air temperature measured by the meteorological station varied between 9.5 and 11.5°C (Fig. 2A), with a high seasonal variability. In addition, average air temperature measured in the 20 stations during the field campaigns ranged from 6 to 32°C. Total rainfall recorded on the site for 2014 and 2015 were quite similar with 935 and 940 mm, respectively (Fig. 2B). The WTL measured by the automatic piezometers ranged between -17.5 and -0.1 cm during the studied period, with clear seasonal variability (Fig. 2C). The average WTL manually measured in the 20 stations during the field campaigns showed a similar cyclicity (Fig. 2C) with deeper level during summer (maximum depth of -18 and -10.5 cm in 2013 and 2014, respectively) than during winter. The seasonal variability of vegetation was controlled by the graminoids which started to grow earlier in 2014 (April) than in 2013 (May) (Fig. 3). Also, in 2014 the vegetation index (VI) was slightly higher than in 2013, at 0.45 and 0.51 respectively.

3.2 CO_2, CH_4 and DOC fluxes

Results of CO_2 fluxes (NEE, ER and calculated GPP) are presented in Fig. 2. CO_2 fluxes (GPP and ER) showed a clear seasonal trend with a maximum in summer. In 2013 the GPP averaged maximum occurred at the end of July reaching 12.80±4.91 µmol m^{-2} s^{-1} and ER 9.43±3.48 µmol m^{-2} s^{-1}, with the maximum of both variables reached at the end of July (Fig. 2A and B). In 2014 the GPP and ER averaged maxima were reached earlier, in June with 13.16±4.70 µmol m^{-2} s^{-1} and 7.83±2.55 µmol m^{-2} s^{-1} respectively (Fig. 2A and B). Averages values of GPP for 2013 and 2014 were 7.12±5.19 and 6.56±4.72 µmol m^{-2} s^{-1} respectively. For ER, the average values were, for 2013 and 2014, 4.27±3.16 and 3.63±2.56 µmol m^{-2} s^{-1}, respectively (Fig. 4 A and B). Mean values of NEE for 2013 and 2014 were 2.85±3.05 and 2.93±2.77 µmol m^{-2} s^{-1}, respectively (Fig. 4 C). In comparison to CO_2, CH_4 emissions showed a lower magnitude with fluxes below 0.3 µmol m^{-2} s^{-1}. A clear difference was also visible between 2013 and 2014 respectively (Fig. 5). In 2013 CH_4 average fluxes were 0.04±0.03 µmol m^{-2} s^{-1}, whereas they reached 0.10±0.08 µmol m^{-2} s^{-1}in 2014. For both years, the average DOC concentrations measured at the outlet of the peatland were 18.5±7.7 mg L^{-1}. Thus, the average cumulated flux of DOC leaving the peatland for 2013 and 2014 was 12±1 gC m^{-2} yr^{-1} (8±1 and 16±1 gC m^{-2} yr^{-1} in 2013 and 2014, respectively).

3.3 Model selection

Comparisons between modelled and measured values of ER, GPP and CH_4, using models 1 and 2 during calibration and evaluation are presented in Fig. 6. During models' calibration, incorporation of vegetation in the ER model (leading to ER-2) improved the representation of ER, yielded to a higher

R^2 and a lower NRMSE than without vegetation (ER-1, Fig. 6A and Table 1). However, the difference between ER-1 and ER-2 is low but the AIC, which decreased from 47 to 35, confirmed this observation (Table 1). ER was estimated to 1286±231 and 1261±164 gC m^{-2} yr^{-1} for ER-1 and ER-2, respectively. Concerning GPP, GPP-2 realized a higher R^2_a score, a lower NRMSE, and a lower AIC compared to GPP-1 (Fig. 6C and Table 1). Resulting cumulated fluxes were 1290±400 and 1070±203 gC m^{-2} yr^{-1} for GPP-1 and GPP-2. For CH_4, only CH_4-2 (including vegetation) that showed a satisfying result (Fig. 6E and Table 1) was used to estimate the CH_4 cumulated fluxes. Evaluation of the GPP models showed high NRMSE values with 47 and 58 % for GPP-1 and GPP-2 respectively (Fig. 6D and Table 1). CH_4 evaluation led to even higher NRMSE values with 68 % for F_{CH4}-2. R^2_a negative values due to the use of non-linear regression were here irrelevant (Fig. 6F and Table 1). On the contrary, the ER models led to high R^2_a and low NRMSE values with ER-2 performing better than ER-1: R^2_a values increased from 0.16 to 0.59 and NRMSE values decreased from 35 to 23 % (Fig. 6E and Table 1).

3.4 Calculation of Net Ecosystem Carbon Balance (NECB)

NECB (estimated here as GPP-ER-F_{CH4}-F_{DOC}) was calculated first without inclusion of vegetation in the model (GPP-1, ER-1) and then with vegetation (GPP-2, ER-2), at the exception of the calculation of CH_4 for which only the model with vegetation was used (CH_4-2). Whether model 1 or 2 was used, the NECB showed that the peatland was a source of carbon to the atmosphere in 2013 and 2014 with -26 gC m^{-2} yr^{-1} and -220 gC m^{-2} yr^{-1} for model 1 or 2, respectively (Table 2). The high difference in the estimation of NECB was principally due to the GPP estimations (Table 1). In addition, NECB was higher in 2013 than in 2014 (Table 2). NECB was mainly driven by CO_2 fluxes as CH_4 and DOC fluxes are two orders of magnitude lower. However, in terms of the Global Warming Potential (GWP), CH_4 fluxes are not negligible with CH_4 having a GWP 34 times higher than CO_2 for the 100-year time horizon (Myhre *et al*, 2013).

3.4 Spatial variability

The calibration of ER-2 and GPP-2 on each measurement plot enabled the spatial variability of the CO_2 fluxes on the site to be estimated. For ER-2, the R^2_a of the individual plots were above 0.5 (with the exception of measurement plot n°10) and the NRMSE values were below 50% (Fig. 7). The model parameter variations ranged from 0 to 0.015 for a, from 0.035 to 0.11 for b, and from 0.18 to 1.03 for c. For GPP-2 the R^2_a were above 0.5 and the NRMSE values between 20 and 60% (with the exception of point n°10). Model parameters for GPP-2 showed higher variations: between -6.1 and 66 for a, 23.9 and 90.4 for b, 6.2 and 60.0 for c and -10.7 and 27.1 for d (Fig. 8). For both measurement years, cumulated GPP fluxes ranged from 511 to 1420 gC m^{-2} yr^{-1}, with most values around 1100 gC m^{-2} yr^{-1} and an average of 1052±238 gC m^{-2} yr^{-1}. For ER, the cumulated fluxes ranged from 842 to 2363 gC m^{-2} yr^{-1} with an average of 1215±362 gC m^{-2} yr^{-1} (Fig. 7 and 8).

4. Discussion

4.1 Rationale behind the high C fluxes recorded and the C source functioning

CO_2 fluxes measured at La Guette peatland were above 1000 gC m^{-2} yr^{-1} for the GPP and the ER, whatever the model used. These fluxes were high compared to those of boreal peatlands. Trudeau *et al.* (2014) and Peichl *et al.* (2014) found GPP and ER fluxes between 100 and 500 gC m^{-2} yr^{-1} approximately for sites located in Quebec, Canada and in Northern Sweden respectively. However, these large fluxes were close to those found for sites with a high Mean Annual Temperature (MAT). For instance, Beyer and Höper (2015) found for a site with similar vegetation (*Molinia caerulea*, *Eriophorum augustifolium*, *Sphagnum* spp.) and with a MAT of 8.6°C, GPP fluxes between 534 and 1058 gC m^{-2} yr^{-1} and ER fluxes between 420 and 1052 gC m^{-2} yr^{-1}. Thus, the large fluxes measured in La Guette peatland can be related to the relatively warmer climate compared to peatlands at higher latitudes. However, a MAT alone cannot explain why the system functioned as a source of C as other studies have shown that peatlands with a MAT above 8°C can still be a C sink. For instance, Koehler *et al.* (2011) estimated an uptake of -29.7 gC m^{-2} yr^{-1} in an Atlantic blanket bog with a MAT of 10.6°C for a 6-year average (2003-2008). The water table drawdown favours oxic reactions in a thicker soil layer, thus it is often adduced to explain the sources of C in peatlands. During the two years of measurements, La Guette peatland experienced favourable hydrological conditions due to heavy rainfall leading to high water table levels (Bernard-Jannin *et al*, 2018). In spite of this, the system functioned as a source to the atmosphere. Moreover, these high water table levels was spatially and temporally similar during the time course of the experiment (2013-2014, two exceptionally wet years), which did not allow to include this factor during the modelling processes. Higher variation of the water table depth could have brought to use equations with this parameters as Luan et al. (2015) to explain the GPP or Leroy et al. (2019) to model the CO_2 and CH_4 emissions. Nevertheless, inclusion of environmental parameters have to be considered up to their contribution to the models and to the models parsimony (Baird et al., 2019).

This C source function if the La Guette peatland is now also shown thanks to an Eddy-covariance tower and this with C fluxes similar as reported here (Jacotot et al., in prep). The main hypothesis concerning the mechanisms behind the C source function of the La Guette is linked to recent invasion of the site by *Molinia caerulea*, which is suspected to modify the C dynamic of the ecosystem. The observed C flux intensities and losses are often related to the plant community of the peatland. Vascular plants have higher gaseous C fluxes than bryophytes in poor fens (Leroy *et al,* 2019; Rydin and Jeglum, 2013) and a shift in peatland plant communities, especially those reducing *Sphagnum* dominance in favor of vascular vegetation, is expected to have significant effects on carbon storage (Dieleman et al., 2015). Now, the site is almost entirely invaded by vascular plants, especially *Molinia caerulea* in the graminoid strata (Gogo *et al,* 2011). The occurrence of this plant can stimulate the C uptake compared to *Sphagnum* peatland (Leroy et al., 2019). However it also significantly increase the ER respiration and CH_4 emissions through different physiological, phenological, and ecological traits (Gogo et al., 2011; Leroy et al., 2019). The ratio GPP/ER should be further assessed, especially in the context of interaction between different functional types (D'Angelo, 2015)

4.2 Implication of taking vegetation into account in the C budget estimation

The plants functional type often explained large of variation of the CO_2 and CH_4 fluxes (Armstrong et al., 2015). In this way, it was thus important to include the vegetation in our models, especially with the occurrence of *Molina caerulea*. Indeed, this species shows a high growth variability during the growing season (e.g. number of leaves, leave length) that could impact the C fluxes (more leaves, more GPP). However, its integration into models is seldom carried out (Bortoluzzi et al., 2006; Görres et al., 2014), probably because of the difficulty in measuring the pertinent variables (leaf area index, leaves number). Including vegetation in models has led to a better representation of CO_2 fluxes. These results were in accordance with Bortoluzzi *et al.* (2006) who also found a lower NRMSE when vegetation was included in the model. Another way to take the vegetation into account is to use the Ratio Vegetation Index (RVI), which is a measurement of incoming and reflected radiation. This method was used by Görres *et al.* (2014) and led to an improvement for GPP modelling but not for ER. However, such an improvement using the RVI for ER modelling was found by Kandel *et al.* (2013) on a cultivated fen peatland in Denmark. Although the calibration of the model was as good for ER as for GPP, evaluation of the models presented more contrasted results since only ER-2 showed a high R^2_a and a low NRMSE. For F_{CH4}-2 the evaluation revealed that the interpretation of the model outputs should be limited to the current study and could not be used to extrapolate fluxes for other times and spaces. Nevertheless, as hypothesis, model evaluations indicated that the inclusion of vegetation increased the model's capability to represent CO_2 fluxes.

4.3 The DOC exports

The quantities of DOC exported by La Guette peatland are in the same order of magnitude of those present in the literature (e.g. Waddington and Roulet, 2000; Worrall., 2009) but have a low impact on C balance compared to CO_2 fluxes. The doubling of the DOC flux observed in 2014 compared to 2013 is linked to a greater quantity of water leaving the bog with similar DOC contents. At the same time, the average water table measured in 2014 is slightly higher than that measured in 2013 and precipitation is of the same order of magnitude (Fig. 2).

4.4 ER and GPP spatial variability

Calibration of the individual CO_2 fluxes at the 20 measurement points showed a large range of cumulated flux estimation (Fig. 7 and 8). Nonetheless, the average of these fluxes was coherent with those estimated at the ecosystem scale with the average of the 20 points: 1215 *vs.* 1261 gC m^{-2} yr^{-1} and 1052 *vs.* 1070 for ER and GPP respectively (Table 1). The ER estimates are very close for the two years, which is consistent with the relatively similar water table also observed. The difference in air temperature between 2013 and 2014 (9.1 and 10.1 ◦C respectively) is not sufficient to observe a significant difference. The order of magnitude of the spatial variability was the same between ER and GPP estimated within one site (this study) and ER and GPP estimated in different sites by Jacobs *et al.* (2007). For ER, the spatial variability found within La Guette peatland was also larger than the inter-annual variability measured by Beyer *et al.* (2015), in which the difference between the maximum and minimum annual fluxes was 429 gC m^{-2} yr^{-1} on a temperate fen used as grassland. With the acquired data, no patterns have been found between the location of the points and the model parameters or with the measured environmental variables that would enable this spatial variability to be linked to specific local environmental conditions. Indeed, this variability does not seem geographically distributed or related to gradient of environmental parameters with spatial and temporal similarity of the air temperature and water table levels. However, a first approach by grouping points per vegetation classes (with dominance of the muscular, herbaceous or shrubs strata) shows promising results in order to explain this spatial variability (D'Angelo, 2015).

Conclusions

In this study we have shown that despite high water table levels, La Guette peatland acted as a C source to the atmosphere for the 2 years of measurements, in 2013 and 2014. This was partly explained by the high mean annual temperatures that led to large fluxes. However, it is probable that the site history also played a significant role: after several dry years, the peatland was just starting to refill during the 2 measurement years, probably leading to air trapped in the porosity that favoured oxic organic matter degradation. Longer observations are needed to catch the long-term dynamics in terms of hydrological cycle and site history leading to hysteresis effects. The vegetation had a significant effect when included in ER models despite the difficulty in monitoring the vegetation profile without disturbances. However, such an effect was not as clear for the GPP models. As a result, the ER models had a narrower range of estimations (more precise when vegetation is included) than the GPP ones, indicating that ER models seem more reliable. As a result, this study advocates the inclusion of vegetation in models, even in a simplistic way. These results also emphasize the importance of model evaluation as it outcomes may be quite different from the calibration and this even for models with very well-fitted parameters. Accessing these differences might help to estimate the interpretative power of such models in a broader context. Finally, the estimations of the CO_2 fluxes on the 20 measurement points showed a large spatial variability. The order of magnitude of this variability estimated on one site was the same as those reported between different sites. More studies are needed to better quantify the spatial variability within a site, and to allow a better estimation of the uncertainty of the greenhouse gas budget estimated at larger scales.

Author contribution.

BD, SG and FLD designed the experiment

BD, SG, CG, FL and FLM collected data

BD, SG, CG, FL and FLM performed model simulations and data analysis

BD and FL prepared the manuscript with contributions from all co-authors

AJ and RZ reviewed and corrected the manuscript

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