



CO₂ and CH₄ budgets and global warming potential modifications in *Sphagnum*-dominated peat mesocosms invaded by *Molinia caerulea*

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Abstract. Plant communities play a key role in regulating greenhouse gas (GHG) emissions in peatland ecosystems and therefore in their ability to act as carbon (C) sinks. However, in response to global change, a shift from *Sphagnum*-dominated to vascular-plant-dominated peatlands may occur, with a potential alteration in their C-sink function. To investigate how the main GHG fluxes (CO₂ and CH₄) are affected by a plant community change (shift from dominance of *Sphagnum* mosses to vascular plants, i.e., *Molinia caerulea*), a mesocosm experiment was set up. Gross primary production (GPP), ecosystem respiration (ER) and CH₄ emission models were used to estimate the annual C balance and global warming potential under both vegetation covers. While the ER and CH₄ emission models estimated an output of, respectively, 376 ± 108 and 7 ± 4 g C m⁻² yr⁻¹ in *Sphagnum* mesocosms, this reached 1018 ± 362 and 33 ± 8 g C m⁻² yr⁻¹ in mesocosms with *Sphagnum rubellum* and *Molinia caerulea*. Annual modeled GPP was estimated at -414 ± 122 and -1273 ± 482 g C m⁻² yr⁻¹ in *Sphagnum* and *Sphagnum* + *Molinia* plots, respectively, leading to an annual CO₂ and CH₄ budget of -30 g C m⁻² yr⁻¹ in *Sphagnum* plots and of -223 g C m⁻² yr⁻¹ in *Sphagnum* + *Molinia* ones (i.e., a C sink). Even if CH₄ emissions accounted for a small part of the gaseous C efflux (ca. 3 %), their global warming potential value makes both plant communities have a climate warming effect. The shift of vegetation from *Sphagnum* mosses to *Molinia caerulea* seems beneficial for C sequestra-

tion at a gaseous level. However, roots and litter of *Molinia caerulea* could provide substrates for C emissions that were not taken into account in the short measurement period studied here.

1 Introduction

Peatlands are wetlands that act as a carbon (C) sink at a global scale. They cover only 3 % of the land area but have accumulated between 473 to 621 Gt C (Yu et al., 2010), representing 30 % of the global soil C. The C-storage capacity of northern peatlands is closely linked to environmental conditions and plant cover characteristics which limit the activity of soil decomposers. As a result, in spite of the relatively small net ecosystem production in peatlands, the imbalance between primary production and decomposition is enough to allow high organic matter (OM) accumulation as peat (Bragazza et al., 2009). Accumulating *Sphagnum* litter forms a major component of peat (Turetsky, 2003) and creates acidic, nutrient-poor, wet and anoxic conditions that favor the peat accumulation. Thus, *Sphagnum* species are able to outcompete vascular plants and reduce microbial decomposition (van Breemen, 1995). However, due to global change, environmental modifications (nutrient input, water table drop, warmer climate, etc.) are expected to cause a plant community shift in peatlands, with an increase in vascular

plants (especially graminoids) to the detriment of *Sphagnum* species (Berendse et al., 2001; Buttler et al., 2015; Dieleman et al., 2015). Vascular plant invasion could lead to a faster decomposition of peat OM due to a change in litter quality as a substrate for decomposers, thereby decreasing C sequestration (Strakova et al., 2011). Furthermore, OM already stored in deep peat may be subject to increased decomposition through the stimulating effect of rhizospheric C input (Girkin et al., 2018). If these losses are not compensated by increased gross primary productivity, peatlands could shift from a sink to a source of C and could increase greenhouse gas emissions, mainly carbon dioxide (CO₂) and methane (CH₄). Vascular plant invasion in peatlands has mostly been studied through a change in decomposition rates (Moore et al., 2007; Gogo et al., 2016) and modification in decomposer activities (Krab et al., 2013; Strakova et al., 2011). Some studies have paid attention to CH₄ emissions with and without the presence of *Carex* or *Eriophorum* (Noyce et al., 2014; Green and Baird, 2012; Greenup et al., 2000) and to CO₂ fluxes with different plant community compositions (Neff and Hooper, 2002; Ward et al., 2013). In spite of observed changes in C fluxes, the role of vascular-plant invasion in the C balance in peatlands remains to be elucidated. The aim of this study was to investigate how an invading graminoid species, *Molinia caerulea*, can affect the greenhouse gas C budget (GGCB) of a *Sphagnum*-dominated peatland. *Molinia caerulea* encroachment is a well-acknowledged problem in Europe linked to anthropogenic pressures such as nutrient deposition and management practices, but studies of the effects on peatland ecosystem are still limited (Ritson et al., 2017; Berendse et al., 2001; Chambers et al., 1999). Here, CO₂ fluxes and CH₄ emissions were regularly measured in mesocosms entirely covered by *Sphagnum rubellum* with or without *Molinia caerulea* during 14 months and were related to biotic and abiotic factors to estimate the annual C budget. The experimental design and a part of the data have been used in Leroy et al. (2017, 2019) to explore different questions than those explored in the present paper: the temperature sensitivity and N-deposition effect on the C and N cycle with two different plant communities in peatlands, respectively. In this paper, the novelty was (1) treatment of the GPP data (which was not done in any of the other two published papers) and (2) the modeling of the C fluxes (GPP, ecosystem respiration – ER – and CH₄ emissions) to estimate, in fine, the C balance under these two plants communities. Such C budget calculation allowed the estimation of the global warming potential, a key feature of the paper, which was not studied in the previous papers and deserves attention on its own.

2 Materials and methods

2.1 Experimental design, sampling and methods

Twelve cylindrical peat mesocosms (30 cm in thickness and diameter) and water were collected in La Guette peatland (France) in March 2015. The site is a *Sphagnum*-dominated transitional fen that was invaded by *Molinia caerulea* and *Betula* spp. (*Betula verrucosa* and *Betula pubescens*), promoted by hydrological disturbances and nutrient inputs (Gogo et al., 2011). The mesocosms were buried near the laboratory in mineral soil, with a waterproof tarpaulin containing peat water surrounding them. Environmental conditions were monitored with a weather station, including solar radiation, relative humidity, and air and soil temperature at the 5 and 20 cm depth every 15 min. The mesocosms were separated into two treatment groups: six mesocosms containing only *Sphagnum rubellum* (called “*Sphagnum*” plots) and six containing both *Sphagnum rubellum* and *Molinia caerulea* (called “*Sphagnum* + *Molinia*” plots). All mesocosms were entirely and exclusively covered by *Sphagnum rubellum*. *Molinia caerulea* appeared in May and increased up to 60 % of mesocosms on average until its senescence in November (Leroy et al., 2017) and did not affect *Sphagnum* cover (unpublished data). *Molinia caerulea* seedlings (roots and stems) were manually removed from *Sphagnum* plots. The water table level (WTL) was measured by a piezometer installed within each mesocosm and was maintained between 5 and 10 cm depth with addition of peat water when necessary. The number and height of *Molinia caerulea* leaves were measured.

2.2 Greenhouse gas measurements

Measurements were performed with the static chamber method from May 2015 to June 2016. The global principle of this method is to pose a hermetic chamber on the mesocosms in order to monitor the gas concentrations inside this chamber from which gas fluxes between soil and atmosphere can be calculated. Here, CO₂ and CH₄ fluxes were measured once or twice per week during the growing season (April–October 2015 and April–June 2016) and every 2 weeks during the winter (November 2015–March 2016). The measurement was usually performed between 09:00 and 17:00 LT. Here, the effect of diurnal cycle on fluxes that is supposed to be taking the modeling processes into account because of this diurnal variation seems related to the environmental parameters (Wright et al., 2013). The CO₂ and CH₄ emissions reported here are also used in Leroy et al. (2017) to discuss their temperature sensitivity but used for only 1 year of measurement (from May 2015 to April 2016). Here, these emissions are used to establish a C balance to complement the GPP. CO₂ concentrations were estimated using a GMP343 Vaisala probe inserted into a transparent PVC chamber (D’Angelo et al., 2016; Leroy et al., 2017). This clear chamber was used to measure the net ecosystem ex-

change (NEE), the balance between gross primary production (GPP; absorption of CO₂ by photosynthesis) and ER (release of CO₂ into the atmosphere). ER was measured by placing an opaque cover on the chamber to block photosynthesis. The difference between NEE and ER corresponded to the GPP. The measurements lasted a maximum of 5 min, and CO₂ concentration was recorded every 5 s. The slope of the relationship between CO₂ concentration and time allowed for fluxes (in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) to be calculated. CH₄ emissions were measured using SPIRIT, a portable infrared laser spectrometer (Guimbaud et al., 2016), measuring CH₄ concentration in a transparent chamber. Measurements take several to 20 min, with a time resolution of 1.5 s (Guimbaud et al., 2011).

2.3 Carbon flux modeling

2.3.1 Ecosystem respiration

The ER increased with increasing air temperature and decreasing WTL in both vegetation covers (Supplement), as found by Bortoluzzi et al. (2006). Here, in order to improve the data analysis from Leroy et al. (2017) and establish a C balance, the ER was derived for the entire year by using the equation from Bortoluzzi et al. (2006) for *Sphagnum* plots (Eq. 1):

$$\text{ER}_{\text{sph}} = \left[a \cdot \frac{\text{WTL}}{\text{WTL}_{\text{ref}}} + b \right] \cdot \left(\frac{(T_a - T_{\text{min}})}{(T_{\text{ref}} - T_{\text{min}})} \right)^c \quad (1)$$

ER is the ecosystem respiration flux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). T_{ref} is the reference air temperature and T_{min} the minimum air temperature. These two parameters were set as in Bortoluzzi et al. (2006) at 15 and -5°C , respectively. T_a refers to the measured air temperature ($^\circ\text{C}$). The reference for the WTL (WTL_{ref}) was set at -15 cm , corresponding to the deepest WTL recorded in the mesocosms. The coefficients a , b and c (temperature sensitivity parameters) are empirical parameters.

In *Sphagnum* + *Molinia* plots, ER was significantly correlated to the number of *Molinia caerulea* leaves ($r^2 = 0.44$; Supplement). Following Bortoluzzi et al. (2006) and Kandel et al. (2013), we included, in addition to WTL and temperature, a vegetation index based on the number of *Molinia caerulea* leaves in the ER model for *Sphagnum* + *Molinia* plots (Eq. 2):

$$\text{ER}_{\text{mol}} = \left[\left(a \cdot \frac{\text{WTL}}{\text{WTL}_{\text{ref}}} \right) + (b \cdot \text{Mc}_{\text{leaves}}) \right] \cdot \left(\frac{(T_a - T_{\text{min}})}{(T_{\text{ref}} - T_{\text{min}})} \right)^c \quad (2)$$

$\text{Mc}_{\text{leaves}}$ is the number of *Molinia caerulea* leaves.

2.3.2 Gross primary production

The relationship between GPP and photosynthetic photon flux density (PPFD) is often described by a rectangular hy-

perbolic saturation curve with

$$\text{GPP} = \frac{i \cdot \text{PPFD} \cdot \text{GPP}_{\text{max}}}{i \cdot \text{PPFD} + \text{GPP}_{\text{max}}}, \quad (3)$$

where i ($\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ per photon) is the initial slope of the hyperbola, GPP_{max} is the maximum GPP ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) and PPFD is the photosynthetic photon flux density ($\mu\text{mol m}^{-2} \text{ s}^{-1}$). This approach was modified by Mahadevan et al. (2008) and Kandel et al. (2013) to include the effect of temperature and vegetation on the GPP model. The vegetation index was implemented ($\text{Mc}_{\text{leaves}}$) in the models after studying the relationship between GPP and photosynthetic photon flux density at different vegetation stages (described in Results; Figs. 2 and S1). The same equation was used in this study (Eq. 4):

$$\text{GPP} = \frac{\text{GPP}_{\text{max}} \cdot \text{PPFD}}{k + \text{PPFD}} \cdot \text{Mc}_{\text{leaves}} \cdot T_{\text{scale}}, \quad (4)$$

where GPP_{max} ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) represents the GPP at light saturation, the parameter k ($\mu\text{mol m}^{-2} \text{ s}^{-1}$; Eq. 4) is the half-saturation value, and $\text{Mc}_{\text{leaves}}$ is the number of *Molinia caerulea* leaves. T_{scale} is the temperature sensitivity of photosynthesis based on Kandel et al. (2013) and calculated as

$$T_{\text{scale}} = \frac{(T - T_{\text{min}})(T - T_{\text{max}})}{(T - T_{\text{min}})(T - T_{\text{max}}) - (T - T_{\text{opt}})^2}, \quad (5)$$

where T is the air temperature measured with the weather station, and T_{min} , T_{opt} and T_{max} represent the minimum, optimum and maximum air temperature for photosynthesis, which were set at 0, 20 and 40°C , respectively.

2.3.3 CH₄ emissions

The CH₄ emissions were significantly correlated to the soil temperature and the water table level (Leroy et al., 2017; Supplement). An equation similar to Eq. (1) was used to model the emissions (Eq. 6):

$$\text{CH}_4 = \left[d \cdot \frac{\text{WTL}}{\text{WTL}_{\text{ref}}} + e \right] \cdot \left(\frac{(T_s - T_{\text{min}})}{(T_{\text{ref}} - T_{\text{min}})} \right)^f, \quad (6)$$

where WTL_{ref} , T_{min} , T_{ref} and T_{min} were set as for the ER equation. T_s refers to the measured soil temperature ($^\circ\text{C}$).

2.3.4 Model calibration and validation

Two-thirds of the ER and CH₄ emission measurements (randomly selected) were used to calibrate the equations, and the other third was used for validation in order to verify the calibrated model. Calibration of the GPP models was done using additional measurements, with nets decreasing the PPFD (allowing six GPP measurements under different luminosity per mesocosm) in order to calibrate the GPP_{max} and k parameters based on the Michaelis–Menten equation. In this way, all

measurement points were used to validate the model. Model quality was evaluated using the determination coefficient (r^2) and the normalized root-mean-square error (NRMSE), calculated as

$$\text{NRMSE} = 100 \cdot \frac{\sqrt{\frac{\sum (y - \hat{y})^2}{n}}}{\bar{y}}, \quad (7)$$

where y is the measured value, \hat{y} the computed value, n the number of values and \bar{y} the average of the measured value. The NRMSE indicates the percentage of variance between the measured and the predicted values.

The parameters of ER (a , b and c) and CH₄ emissions (d , e and f) models were calibrated by minimizing the NRMSE using the “SANN” method of the optim function in R (R Core Team, 2016).

2.3.5 Greenhouse gas C budget and global warming potential

The net ecosystem C balance (NECB) represents the net rate of C accumulation or release in or from the ecosystem (Chapin et al., 2006) and is calculated as

$$\text{NECB} = -\text{GPP} + \text{ER} + F_{\text{CH}_4} + F_{\text{CO}} + F_{\text{VOC}} + F_{\text{DIC}} + F_{\text{DOC}} + F_{\text{PC}}, \quad (8)$$

where GPP is the gross primary production ($\mu\text{mol m}^{-2} \text{s}^{-1}$); ER is the ecosystem respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$); and F_{CH_4} , F_{CO} , F_{VOC} , F_{DIC} , F_{DOC} and F_{PC} are the fluxes (in $\text{mmol m}^{-2} \text{s}^{-1}$) of methane (CH₄), C monoxide (CO), volatile organic C (VOC), dissolved inorganic C (DIC), dissolved organic C (DOC) and particulate C (PC), respectively. In this study, we used a simplified approach based on the GPP, ER and CH₄ emissions that we referred to as the GGCB ($\text{g C m}^{-2} \text{yr}^{-1}$). To calculate annual emissions, we run our models with a 15 min time step using continuous weather and vegetation data.

The global warming potential over 100 years (GWP₁₀₀; $\text{g CO}_2 \text{eq. m}^{-2} \text{yr}^{-1}$) was calculated for both plant communities based on the annual greenhouse gas (GHG) fluxes (GPP and ER and the CH₄ emissions) with Eq. (9):

$$\begin{aligned} \text{GWP}_{100} = & (x + y) \cdot \frac{\text{Molecular weight of CO}_2}{\text{Molecular weight of C}} \\ & + z \cdot \frac{\text{Molecular weight of CH}_4}{\text{Molecular weight of C}} \\ & \cdot \text{GWP}_{100} \text{ of CH}_4, \end{aligned} \quad (9)$$

with x and y representing the annual GPP and ER fluxes (in $\text{g C m}^{-2} \text{yr}^{-1}$) and z representing the annual CH₄ emissions (in $\text{g C m}^{-2} \text{yr}^{-1}$). The radiative force (GWP₁₀₀) of CH₄ is 34 times that of CO₂ (Myhre et al., 2013).

2.4 Statistics

The effects of *Molinia caerulea* were assessed by comparing *Sphagnum* + *Molinia* plots to *Sphagnum* plots, with two-

Table 1. Mean values of measurements of net ecosystem exchange (NEE), gross primary production (GPP), ecosystem respiration (ER), CH₄ emissions (CH₄), photosynthetic photon flux density (PPFD), water table level (WTL) and air temperature (T_a) in *Sphagnum* + *Molinia* and *Sphagnum* plots. Significant differences of two-way repeated-measure ANOVAs are expressed as ***, with $p < 0.001$ ($n = 6$). Data are presented as mean \pm SE, where $n = 12$.

	Mean		Significance
	<i>Sphagnum</i>	<i>Sphagnum</i> + <i>Molinia</i>	
GHG fluxes			
NEE ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	-1.15 ± 0.25	-4.63 ± 1.72	***
GPP ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	-2.25 ± 0.40	-7.19 ± 2.28	***
ER ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1.10 ± 0.37	2.56 ± 0.74	***
CH ₄ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0.028 ± 0.013	0.093 ± 0.005	***
Environmental parameters			
WTL (cm)	-5.00 ± 0.70	-6.81 ± 0.63	
PPFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	707 ± 159	669 ± 160	
T _a (°C)	12.27 ± 2.44	12.37 ± 2.49	

way repeated-measure ANOVAs (with plant cover and date as factors).

3 Results

3.1 Environmental conditions

The environmental conditions of our measurements did not significantly differ between *Sphagnum* + *Molinia* and *Sphagnum* plots (Table 1). The only significant differences concern the GHG fluxes, with higher fluxes in *Sphagnum* + *Molinia* plots compared to the *Sphagnum* plots.

3.2 Measured GHG fluxes

ER was significantly higher in *Sphagnum* + *Molinia* plots compared to *Sphagnum* ones. In both vegetation covers, the ER was maximum in July and minimum in January–February (Fig. 1a). GPP increased during the vegetation period (linked to the number of *Molinia* leaves), whereas in *Sphagnum* plots the GPP was relatively constant (Fig. 1b). After the senescence of *Molinia caerulea*, the GPP did not differ between the two treatments, unlike ER, which remained higher in *Molinia* plots compared to *Sphagnum* ones. As a result, the NEE was higher in *Sphagnum* + *Molinia* plots than in *Sphagnum* ones during the growing season but was lower the rest of the time (Fig. 1c). CH₄ emissions significantly increased in *Sphagnum* + *Molinia* plots, with a peak of emissions in summer (June–August) and the lowest emissions in winter (Fig. 1d).

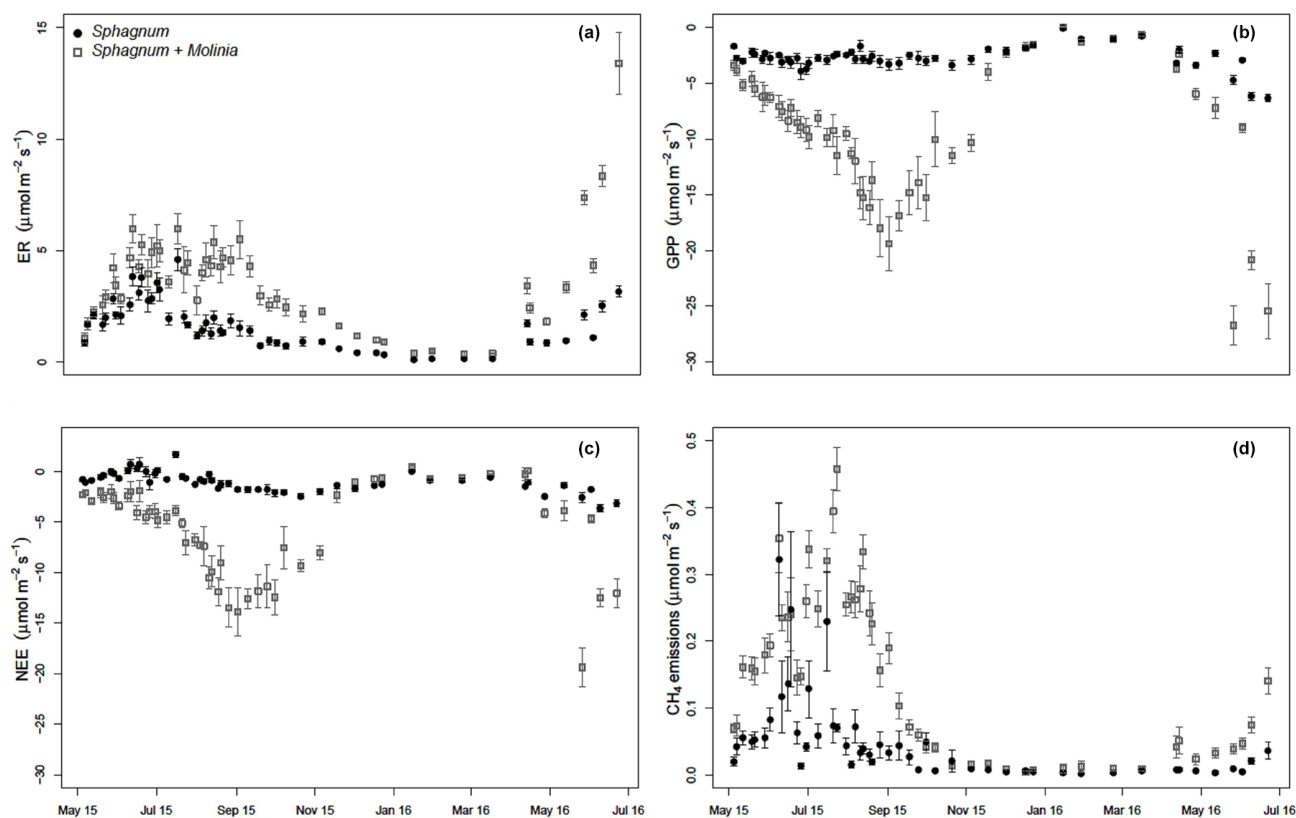


Figure 1. Measurements of ecosystem respiration (ER; **a**), gross primary production (GPP, **b**), net ecosystem exchange (NEE, **c**) and CH₄ emissions (**d**) in *Sphagnum* and *Sphagnum* + *Molinia* plots (\pm SE; $n = 6$) from May 2015 to June 2016.

3.3 Calibration and validation of the GPP models

GPP parameters were calibrated using the photosynthesis–PPFD curves based on the Michaelis–Menten equation using four additional measurements (Fig. 2). The GPP_{max} decreased from -4.6 to $-7.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ in *Sphagnum* plots and from -7.2 in April to $-25.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the end of June in *Sphagnum* + *Molinia* plots.

These increases are linked to *Sphagnum* growth and the number of *Molinia caerulea* leaves, respectively (Supplement). The parameter k ($\mu\text{mol m}^{-2} \text{s}^{-1}$; Eq. 4) is the half-saturation value and was set at the mean k value of the four dates, with k equal to $259 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *Sphagnum* plots and $285 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *Sphagnum* + *Molinia* ones.

Models validations were done using all the measurement points and showed good reproduction of the GPP measurements even if the relatively constant GPP in *Sphagnum* plots had a NRMSE close to 70.

3.4 Calibration and validation of the ER and CH₄ emission models

Calibration of the models showed a good agreement between the modeled and measured ER and CH₄ emissions, with a high r^2 and low NRMSE for both plant communities (Fig. 3).

Regarding the model evaluation, the validation data represented the ER measurements well, especially in *Sphagnum* plots, with a r^2 of 0.82 and a NRMSE of 46.8 (Table 2). However, in *Sphagnum* + *Molinia* plots, the ER model validation showed a r^2 close to 0.6, but with a higher NRMSE. The validation of the CH₄ models explained a good proportion of the variance, with a r^2 of 0.66 in *Sphagnum* plots and of 0.83 in *Sphagnum* + *Molinia* plots (Table 2).

The model parameters a and c , respectively, related to the WTL and temperature sensitivity for ER models, were close for both plant communities, ranging for a from 2.50 to 1.77 and for c from 1.49 to 1.43 in *Sphagnum* and *Sphagnum* + *Molinia* plots, respectively (Table 2). Concerning the parameters of the CH₄ models, d and f differed between the two treatments. The parameter d connected to WTL was positive, at 0.041, in *Sphagnum* plots but negative, at -0.065 , in *Sphagnum* + *Molinia* plots. The f value, representing the temperature sensitivity, rose from 3.32 in *Sphagnum* plots to 5.08 in *Sphagnum* + *Molinia* plots.

3.5 Greenhouse gas carbon budget and global warming potential

The modeled annual GPP over the studied period represented an input of $414 \pm 122 \text{ g C m}^{-2} \text{yr}^{-1}$ in *Sphagnum* plots and

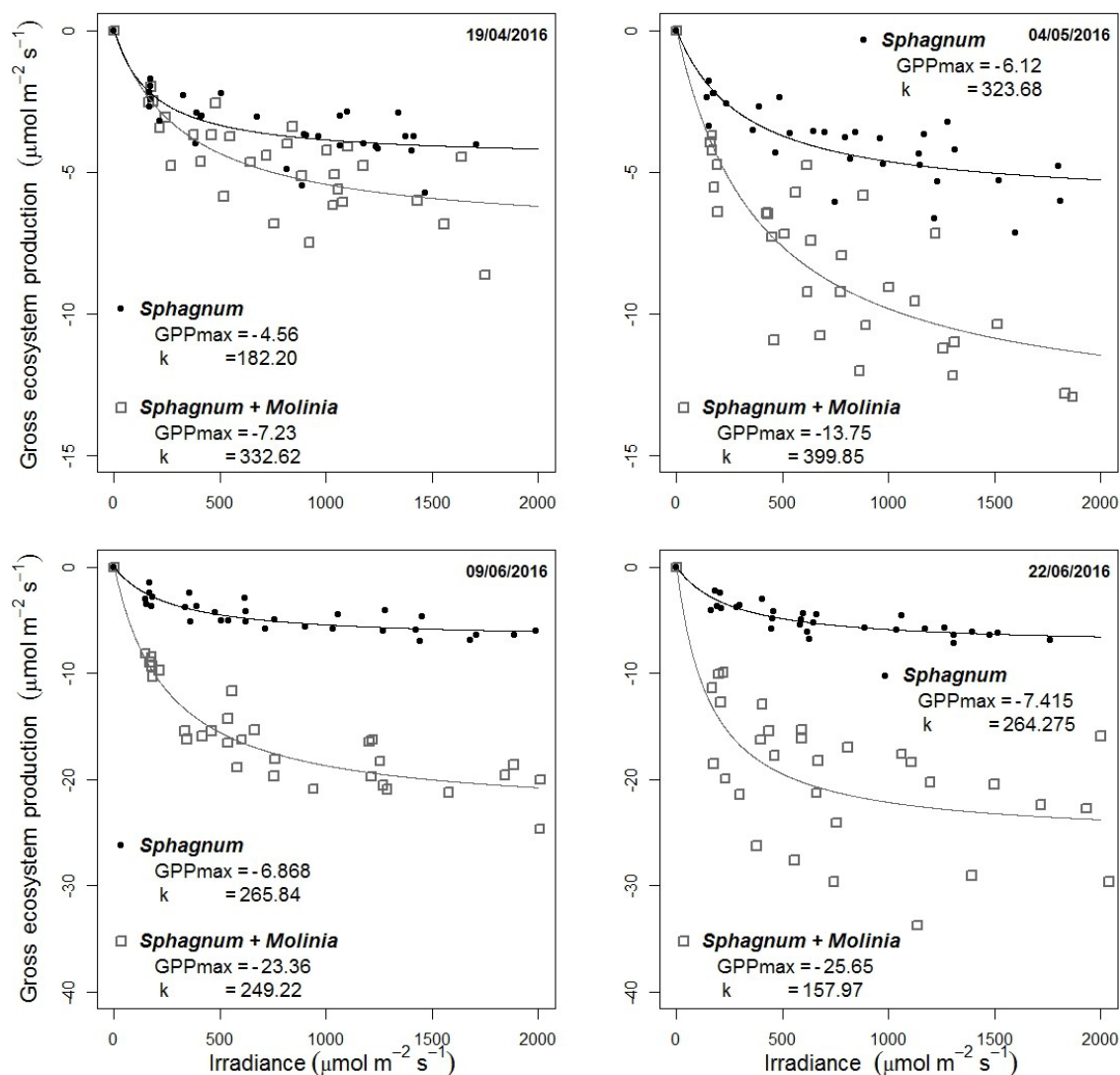


Figure 2. Dependence of gross primary production (GPP) on PPFD on four dates. The photosynthesis–PPFD curve shows the maximum rate of photosynthesis (GPP_{max}) and the half-saturation value (k).

of $1273 \pm 482 \text{ g C m}^{-2} \text{ yr}^{-1}$ in *Sphagnum + Molinia* plots (Table 3). The ER and CH₄ emissions showed, respectively, an output of 376 ± 108 and $7 \pm 4 \text{ g C m}^{-2} \text{ yr}^{-1}$ in *Sphagnum* plots and of 1078 ± 362 and $33 \pm 8 \text{ g C m}^{-2} \text{ yr}^{-1}$ in *Sphagnum + Molinia* plots (Table 3).

From July to December the GGCB was positive in *Sphagnum* plots, which means that these plots released more C than they absorbed, but the GGCB became negative from January to June (Fig. 4). In contrast, the GGCB in *Sphagnum + Molinia* plots was mostly negative, with positive values only in October and November. In the results, the annual GGCB of *Sphagnum* plots absorbed $30 \text{ g C m}^{-2} \text{ yr}^{-1}$, whereas the *Sphagnum + Molinia* plots absorbed $223 \text{ g C m}^{-2} \text{ yr}^{-1}$. The GWP_{100} for *Sphagnum* and *Sphagnum + Molinia* plots was, respectively, +195 and +547 $\text{g CO}_2 \text{ eq. m}^{-2} \text{ yr}^{-1}$.

4 Discussion

4.1 Gaseous C emissions

The presence of *Molinia caerulea* increased the gaseous C fluxes in the *Sphagnum*-dominated peat mesocosms. Compared to these, the GPP was higher with *Molinia caerulea*, with a C uptake close to $1300 \text{ g C m}^{-2} \text{ yr}^{-1}$ against $400 \text{ g C m}^{-2} \text{ yr}^{-1}$ with *Sphagnum* alone. This increase is linked to the large leaf area of *Molinia caerulea*, which increases the photosynthesizing plant material and so the GPP. The estimated GPP of *Sphagnum* mosses is consistent with studies conducted in boreal peatlands, with a GPP close to $350 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Peichl et al., 2014; Trudeau et al., 2014). The GPP calculated with *Molinia caerulea* was higher than that measured in the site at the La Guette peatland, with

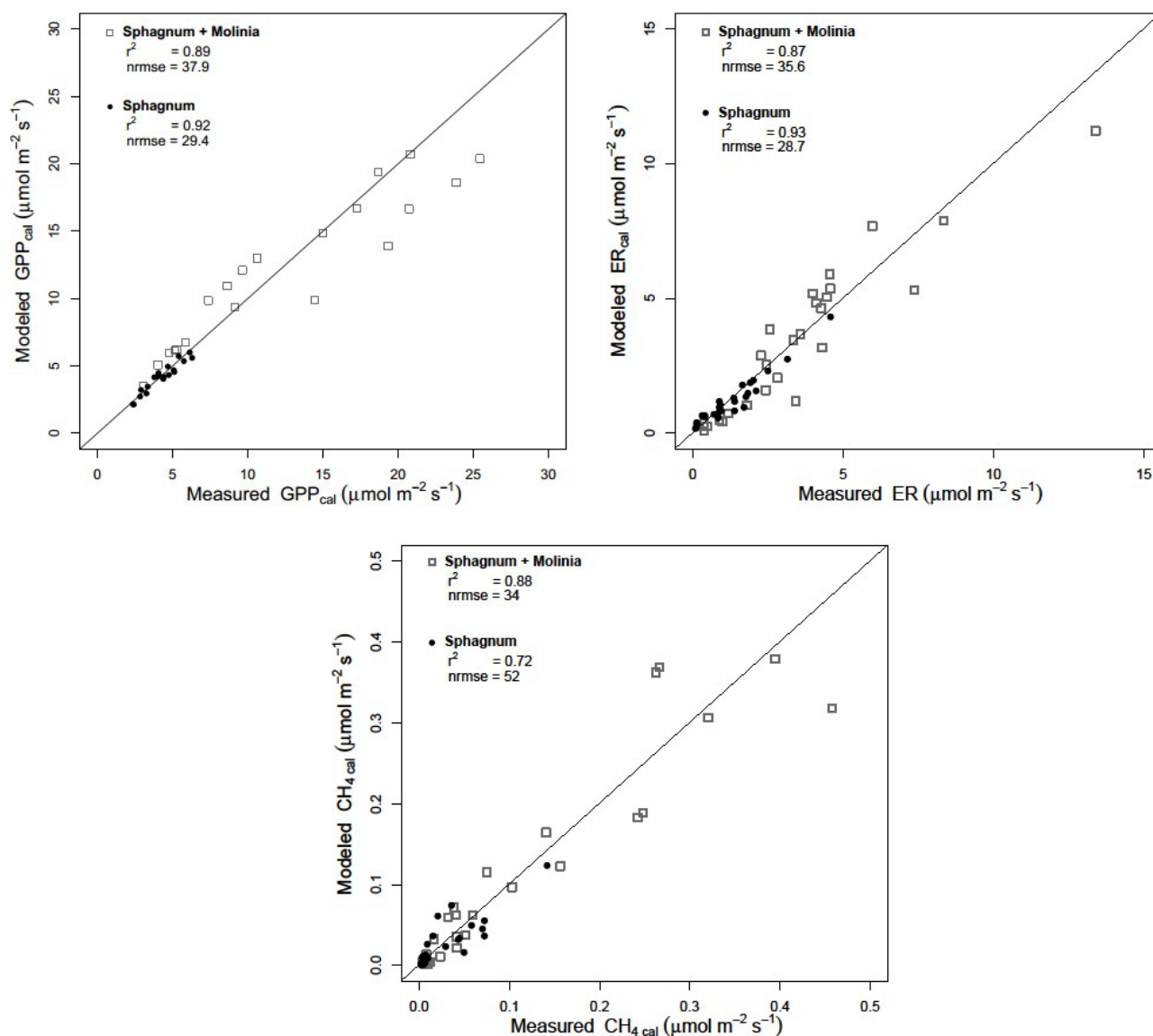


Figure 3. Calibration of the models by comparison of simulated and measured ecosystem respiration (ER), gross primary production (GPP) and CH₄ emission (CH₄) in *Sphagnum* and *Sphagnum + Molinia* plots. The diagonal lines represent the 1 : 1 correlation.

an average of 1052 g C m⁻² yr⁻¹ (D'Angelo, 2015). Such a difference can be explained by the fact that field vegetation in collars contained other types of plants, such as shrubs and woody chamaephytes, that exhibited a lower GPP (D'Angelo, 2015). A higher GPP of vascular plants is expected to modify the belowground interactions that are not taken into account in our models. Indeed, in comparison to *Sphagnum* mosses, vascular plants have an extensive root system which is able to release C and fuel microbial communities to optimize resource allocation (Fenner et al., 2007). It has been shown that up to 40 % of photosynthates can be allocated to root exudates in peatland (Crow and Wieder, 2005), and half of that can be mineralized into CO₂ in a week and promote the ER (Kuzyakov et al., 2001) as the

root decomposition (Ouyang et al., 2017). The higher ER in mesocosms with *Molinia caerulea* can also be linked to the metabolism of this vascular plant itself, in which leaf respiration can account for more than 40 % of the total assimilated C (Kuzyakov et al., 2001). Furthermore, after *Molinia caerulea* senescence, the leaves enhance CO₂ emissions through decomposition. Higher CH₄ emissions with graminoids compared to mosses or shrubs have been explained by the differences in root exudate quality and the aerenchyma of this plant type (e.g., Armstrong et al., 2015).

Table 2. r^2 , normalized root-mean-square errors (NRMSEs) and adjusted model parameters for calibration of ecosystem respiration (ER), gross primary production (GPP), net ecosystem exchange (NEE) and CH₄ emissions (CH₄) in *Sphagnum* + *Molinia* and *Sphagnum* plots.

	Validation	
	<i>Sphagnum</i>	<i>Sphagnum</i> + <i>Molinia</i>
ER		
r^2	0.82	0.59
NRMSE	46.8	94.7
a	2.50	1.77
b	0.33	0.0096
c	1.49	1.43
GPP		
r^2	0.56	0.77
NRMSE	69.2	50.1
CH ₄		
r^2	0.66	0.83
NRMSE	78.5	41.1
d	0.041	−0.065
e	0.001	0.092
f	3.32	5.08

Table 3. Modeled annual gross primary production (GPP; g C m^{−2} yr^{−1}), ecosystem respiration (ER; g C m^{−2} yr^{−1}) and CH₄ emissions (CH₄; g C m^{−2} yr^{−1}) in *Sphagnum* + *Molinia* and *Sphagnum* plots.

	GPP	ER	CH ₄
<i>Sphagnum</i>	−414 ± 122	+376 ± 108	+7 ± 4
<i>Sphagnum</i> + <i>Molinia</i>	−1273 ± 482	+1018 ± 362	+33 ± 8

4.2 Models evaluation and sensitivities to parameters

Evaluation showed that our statistical models were efficient in representing ER and GPP for both plant communities. GPP in *Sphagnum* plots was the most difficult variable to represent (Table 2; Fig. 3). It was quite constant in time, and only a small decrease was observed in winter, when the solar radiation was low. In accordance with Tuittila et al. (2004), the *Sphagnum* growth or cover controlled the photosynthesis. These authors also reported that water saturation of *Sphagnum* governs its photosynthetic capacity and could further improve GPP models (Tuittila et al., 2004). However, with our stable *Sphagnum* moisture and *Sphagnum* cover, GPP in *Sphagnum* plots was mostly controlled by the photosynthetic active radiation. The ER models showed a similar sensitivity in both plant communities to abiotic factors, with an em-

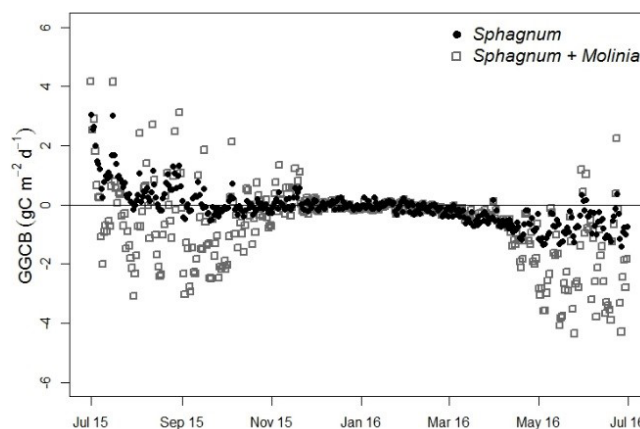


Figure 4. Greenhouse gas carbon budget (GGCB) average per day in *Sphagnum* and *Sphagnum* + *Molinia* plots.

pirical factor related to WTL at 2.1 and a temperature sensitivity close to 1.45 (Table 2). The parameters were similar for both plant communities, and ER differences were mainly due to the contribution of *Molinia* leaves to above-ground and belowground respiration (Kandel et al., 2013). Modeling CH₄ explained a good proportion of the variance (between 70 % and 80 %). The parameters of the CH₄ models differed with vegetation cover. The presence of *Molinia caerulea* increased the temperature sensitivity of CH₄ emissions. Such an increase in the temperature sensitivity could result from modification of methanogenesis pathways. Acetoclastic methanogenesis often dominated in minerotrophic peatlands, as the La Gnette peatland, and required less energy than hydrogenotrophic methanogenesis pathways (Beer and Blodau, 2007). An explication of vascular plants to influence the methane fluxes is often reported for their capacity to supply easily available substrates for the methanogenic microbes and with high variability in substrate quality and availability depending on plants species (Ström et al., 2012). While root exudates are a source of acetate and thus suggested to favor acetoclastic methanogenesis (Saarnio et al., 2004), the root exudates also stimulate the decomposition of recalcitrant organic matter, favoring hydrogenotrophic methanogenesis (Hornibrook et al., 1997) and, maybe more than acetates, promoting acetoclastic methanogenesis. A shift from acetoclastic to hydrogenotrophic methanogenesis pathways could explain the increase in the temperature sensitivity observed here. Contributions of methanogens pathways to methane release could be explored by using mechanistic models. Such models could obtain new insight with additional measurements as substrate supply or microbial community response that could be considered in future studies.

4.3 Annual C fluxes and GGCB

The shift from *Sphagnum*-dominated to *Molinia*-dominated peat mesocosms increased the C fixation through the GPP

but also led to an increase in the annual C output with CO₂ and CH₄ emissions. The gaseous C balance shows that both plant communities act as C sinks, with storage of 30 g C m⁻² yr⁻¹ in *Sphagnum* plots and 223 g C m⁻² yr⁻¹ in *Sphagnum* + *Molinia* plots. These results contrast with the assumption mentioned in the Introduction that vascular plants could lead to a decrease in C sequestration (Strakova et al., 2011). Nevertheless, the C-sink function of *Molinia*-dominated peat mesocosms can be questioned in view of the biomass production of *Molinia caerulea*. The root production, estimated by Taylor et al. (2001) at 1080 g m⁻² yr⁻¹, was produced with current-year photosynthates, meaning that the C allocation in roots could account for 540 g C m⁻² yr⁻¹. Such an amount corresponds to a larger proportion than the C stored in *Sphagnum* + *Molinia* plots (223 g C m⁻² yr⁻¹) and could represent emission of the C already stored. Furthermore, C stored in roots, litter and leaves of *Molinia caerulea* could contribute to future C emissions by decomposition or respiration not taken into account here. Even with this C-sink function, GWP₁₀₀ is positive for both vegetation covers. Although *Sphagnum* + *Molinia* plots act more as a C sink than *Sphagnum* ones, the higher GWP₁₀₀ of CH₄ compared to CO₂ combined with the high emissions of CH₄ for *Sphagnum* + *Molinia* plots lead to a higher contribution of these plots to the greenhouse effect than in *Sphagnum* ones.

The shift from *Sphagnum*-dominated to *Molinia*-dominated peatlands enhanced CO₂ uptake by photosynthesis, which led to higher CO₂ and CH₄ emissions. The application of models taking air temperature, water table level and vegetation index into account described these CO₂ fluxes and CH₄ emissions well. Respiration sensitivity to the two abiotic factors (temperature and WTL) was similar in both communities. However, the presence of *Molinia caerulea* seems to increase the sensitivity of CH₄ emissions to temperature. Modeling the C balance suggested that both *Sphagnum* and *Sphagnum* + *Molinia* plots acted as a C sink. However, belowground C allocation as root C stocks needs further consideration due to its potential role as a substantial C source.

This study demonstrates the implications of *Molinia caerulea* colonization in *Sphagnum* peatland on the C fluxes and on the parameters controlling it. The invasion of numerous peatlands by *Molinia caerulea* will profoundly affect their C cycle at the middle term. However, a better understanding of these effects should be performed by projecting belowground C allocation as root C stocks needs further consideration due to its potential role as a substantial C source.

Data availability. Research data can be accessed by contacting the authors and, soon, through the database of their institution.

Supplement. The supplement related to this article is available online at: <https://doi.org/10.5194/bg-16-4085-2019-supplement>.

Author contributions. FL, SG and FLD designed the experiment. FL, SG, CG, XY, GB and WS collected data. FL, SG, CG, LBJ and FLD performed model simulations and data analysis. FL prepared the paper, with contributions from all co-authors.

Competing interests. The authors declare that they have no conflict of interest.

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