



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* 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 and 7 gC m⁻² y⁻¹ in *Sphagnum* mesocosms, this reached 1018 and 33 gC m⁻² y⁻¹ in mesocosms with *Sphagnum rubellum* and *Molinia caerulea*. Annual modelled GPP was estimated at -414 and -1273 gC m⁻² y⁻¹ in *Sphagnum* and *Sphagnum* + *Molinia* plots, respectively, leading to an annual CO₂ and CH₄ budget of -30 gC m⁻² y⁻¹ in *Sphagnum* plots and of -223 gC m⁻² y⁻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 sequestration at a gaseous level. However, roots and litters 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-sink 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). The major component of peat is the accumulation of *Sphagnum* litter (Turetsky, 2003). *Sphagnum* mosses have a key role in peat accumulation by creating acidic, nutrient poor, wet and anoxic conditions and generating recalcitrant litters. Thus, *Sphagnum* species are able to outcompete vascular plants and reduce microbial decomposition (van Breemen, 1995).
5 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
10 decomposition through the stimulating effect of rhizospheric C input. If these losses are not compensated by an 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
15 *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 on 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 Gases C Budget (GGCB) of a *Sphagnum*-dominated peatland. CO₂ fluxes and CH₄ emissions were regularly measured in *Sphagnum*-peat mesocosms with and without
20 *Molinia caerulea* during fourteen months and were related to biotic and abiotic factors to estimate the annual C budget.

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 has been invaded by *Molinia caerulea* and
25 *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, air and soil temperature at 5 and 20 cm depth every 15 minutes. The mesocosms were separated into 2 treatment groups: 6 mesocosms containing only *Sphagnum rubellum* (called ‘*Sphagnum*’ plots), and 6 containing both *Sphagnum*
30 *rubellum* and *Molinia caerulea* (called ‘*Sphagnum* + *Molinia*’ plots). *Molinia caerulea* appeared in May and increased up to 60% of mesocosms on average until its senescence in November (Leroy et al., 2017). *Molinia caerulea* seedlings were



manually removed from *Sphagnum* plots. The water table level (WTL) was measured by a piezometer installed within each mesocosm. 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. CO₂ and CH₄ fluxes were measured once or twice per week during the growing season (April-October 2015 and April-June 2016) and every two weeks during the winter (November 2015- March 2016). 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 exchange (NEE), the balance between gross primary production (GPP; absorption of CO₂ by photosynthesis) and ecosystem respiration (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 seconds. The slope of the relationship between CO₂ concentration and time allowed fluxes (in μmol CO₂ m⁻² 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 twenty minutes with 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 (Supplementary material), as found by Bortoluzzi et al. (2006). To derive ER for the entire year, the same equation as these authors were used for *Sphagnum* plots (Eq. 1):

$$ER_{sph} = \left[a * \frac{WTL}{WTL_{ref}} + b \right] * \left(\frac{(T_a - T_{min})}{(T_{ref} - T_{min})} \right)^c \quad (1)$$

ER is the ecosystem respiration flux (μmol CO₂ m⁻² 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°C and -5°C, respectively. T_a refers to the measured air temperature (°C). The reference for the WTL (WTL_{ref}) was set at -15cm 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 (r²=0.44; Supplementary material). 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):

$$ER_{mol} = \left[\left(a * \frac{WTL}{WTL_{ref}} \right) + (b * MC_{leaves}) \right] * \left(\frac{(T_a - T_{min})}{(T_{ref} - T_{min})} \right)^c \quad (2)$$



M_{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 hyperbola saturation curve with:

$$5 \quad GPP = \frac{i \cdot PPFD \cdot GPP_{\max}}{i \cdot PPFD + GPP_{\max}} \quad (3)$$

where i ($\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon) is the initial slope of the hyperbola, GPP_{\max} , the maximum GPP ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and PPFD, 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 same equation was used in this study with (Eq. 4):

$$10 \quad GPP = \frac{GPP_{\max} \cdot PPFD}{k + PPFD} * RVI * T_{\text{scale}} \quad (4)$$

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 RVI are a vegetation index to include the effect of *Molinia* leaves number on photosynthesis. T_{scale} is the temperature sensitivity of photosynthesis based on Kandel et al. (2013) and calculated as:

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

15 where T_{\min} , T_{opt} and T_{\max} represent the minimum, optimum and maximum air temperature for photosynthesis and 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 (Supplementary material). An equation similar to Eq. 1 was used to model the emissions (Eq. 6):

$$20 \quad CH_4 = \left[d * \frac{WTL}{WTL_{\text{ref}}} + e \right] * \left(\frac{(T_s - T_{\min})}{(T_{\text{ref}} - T_{\min})} \right)^f \quad (6)$$

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 (°C).

2.3.4 Greenhouse Gases 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:

$$25 \quad \text{NECB} = -\text{GPP} + \text{ER} + \text{F}_{\text{CH}_4} + \text{F}_{\text{CO}} + \text{F}_{\text{VOC}} + \text{F}_{\text{DIC}} + \text{F}_{\text{DOC}} + \text{F}_{\text{PC}} \quad (7)$$

where GPP is the gross primary production ($\mu\text{mol m}^{-2} \text{s}^{-1}$), ER, the Ecosystem Respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and F_{CH_4} , F_{CO} , F_{VOC} , F_{DIC} , F_{DOC} , F_{PC} , the fluxes in $\mu\text{mol m}^{-2} \text{s}^{-1}$ 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 as the Greenhouse Gases C Budget (GGCB, gC m⁻² y⁻¹). The fluxes were modeled at a 15 minutes time step using the calibrated models of GPP, ER and CH₄ emissions. The GGCB was also modeled for a variation in annual temperature from 9.8 to 13.8°C and in WTL from 2.5 to -9 cm, to stimulate increases or decreases in average temperature or WTL by about 2°C and 3 cm, respectively. A simulation of the NEE for

5 *Sphagnum* + *Molinia* plots was also carried out for an elongation or shrinkage of the growing season up to 60 days. Onset and offset occurred during the period of maximum number of *Molinia caerulea* leaves and were combined with a modification in the annual temperature between – and + 2°C, for a mean air temperature between 9.8 and 13.8°C.

The global warming potential over 100 years (GWP₁₀₀; g CO₂ eq m⁻² y⁻¹) was calculated for both plant communities based on the annual GHG fluxes (GPP and ER and the CH₄ emissions) with the Eq. (8):

$$10 \quad GWP_{100} = (x + y) * \frac{\text{Molecular weight of CO}_2}{\text{Molecular weight of C}} + z * \frac{\text{Molecular weight of CH}_4}{\text{Molecular weight of C}} * GWP_{100} \text{ of CH}_4 \quad (9)$$

With x and y representing the annual GPP and ER fluxes (in gC m⁻² y⁻¹), z the annual CH₄ emissions (in gC m⁻² y⁻¹). The radiative force (GWP₁₀₀) of CH₄ is 34 times that of CO₂ (Myhre et al., 2013).

2.4 Statistics and model validation

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

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

Two, randomly select, thirds of the ER and CH₄ emission measurements were used to calibrate the models and the other third was used for validation. Calibration of the GPP models were done using additional measurements with nets decreasing the irradiance (allowing to have 6 GPP measurements under different luminosity per mesocosms) in order to calibrate the GPP_{max}, RVI and k parameters based on the Michaelis-Menten equation. In this ways, all measurement points were used to

20 validate the model. Model quality was evaluated using the determination coefficient (r²) and the Normalized Root Mean Square Error (NRMSE) calculated as:

$$NRMSE = 100 * \frac{\sqrt{\frac{\sum(y - \hat{y})^2}{n}}}{\bar{y}} \quad (9)$$

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.

25 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).



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 annual air mean temperature was 11.8°C and was lower than the average air temperature during the 5 measurements (13.1 °C, Table 1).

Table 1: Mean values of 14 months' measurements of net ecosystem exchange (NEE), gross primary production (GPP), ecosystem respiration (ER), CH₄ emissions (CH₄), photosynthetic active radiation (PAR), water table level (WTL) and air (Ta) and soil temperature (Ts) in *Sphagnum* + *Molinia* and *Sphagnum* plots. Significant differences of two-way repeated-measure ANOVAs are expressed as **p* < 0.05, *p* < 0.01, ****p* < 0.001 (n = 6).**

	Mean		Significativity
	<i>Sphagnum</i>	<i>Sphagnum</i> + <i>Molinia</i>	
GHG fluxes			
NEE (μmol m ⁻² s ⁻¹)	-1.26	-5.22	***
GPP (μmol m ⁻² s ⁻¹)	-2.49	-8.29	***
ER (μmol m ⁻² s ⁻¹)	1.23	3.08	***
CH ₄ (μmol m ⁻² s ⁻¹)	0.030	0.093	***
Environmental parameters			
WTL (cm)	-5.21	-7.05	
PAR (μmol m ⁻² s ⁻¹)	742	718	
Ta (°C)	13.0	13.2	
Ts at 5 cm (°C)	13.9	14.0	
Ts at 20 cm (°C)	14.4	14.2	

10 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 (Table 1, Fig. 1a). GPP increased with 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 that 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 to August) and the lowest emissions in winter (Fig. 1d).

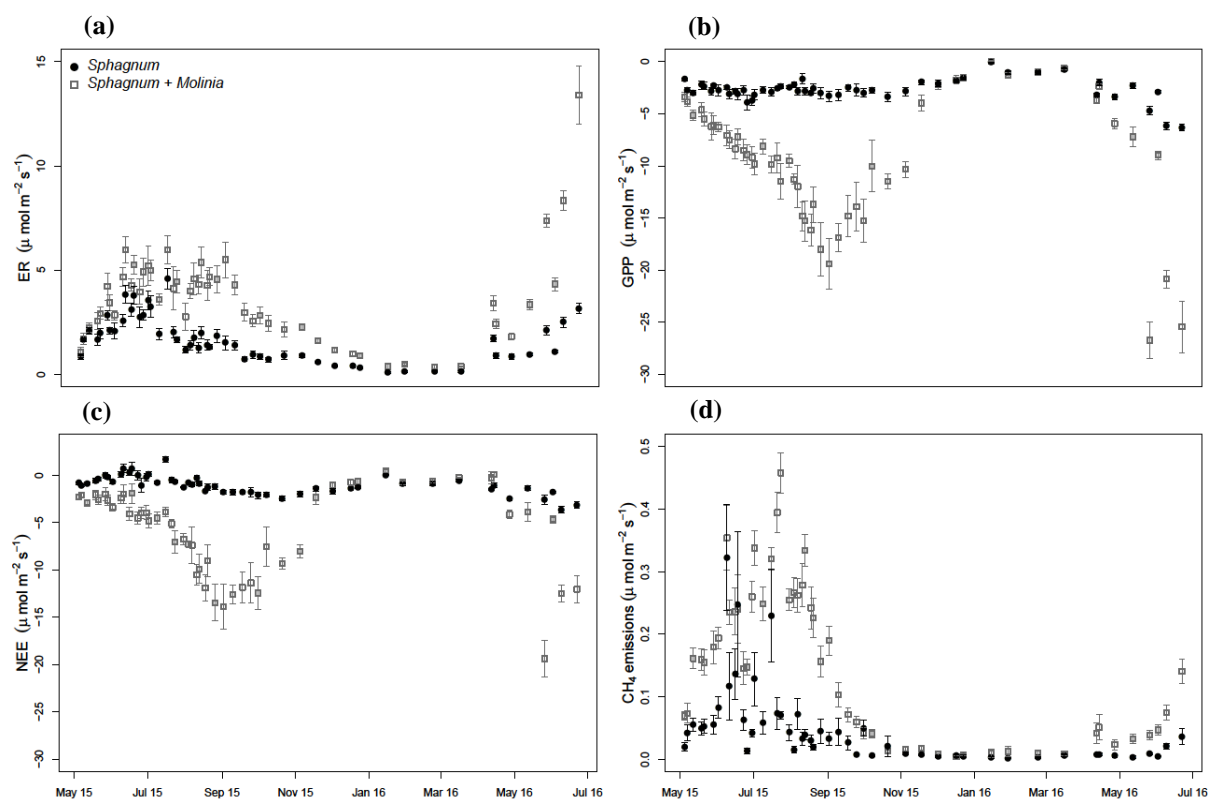


Figure 1: Measurements of ecosystem respiration (ER; a), gross primary production (GPP, b), net ecosystem exchange (NEE, c) and CH₄ emissions (d) in *Sphagnum* and *Sphagnum* + *Molinia* plots (\pm SE, n=6) from May 2015 to June 2016.

3.3 Calibration and validation of the GPP models

GPP parameters were calibrated using the photosynthesis-irradiance curves based on the Michaelis-Menten equation using four additional measurements (Fig. 2). The GPP_{max} increased 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.

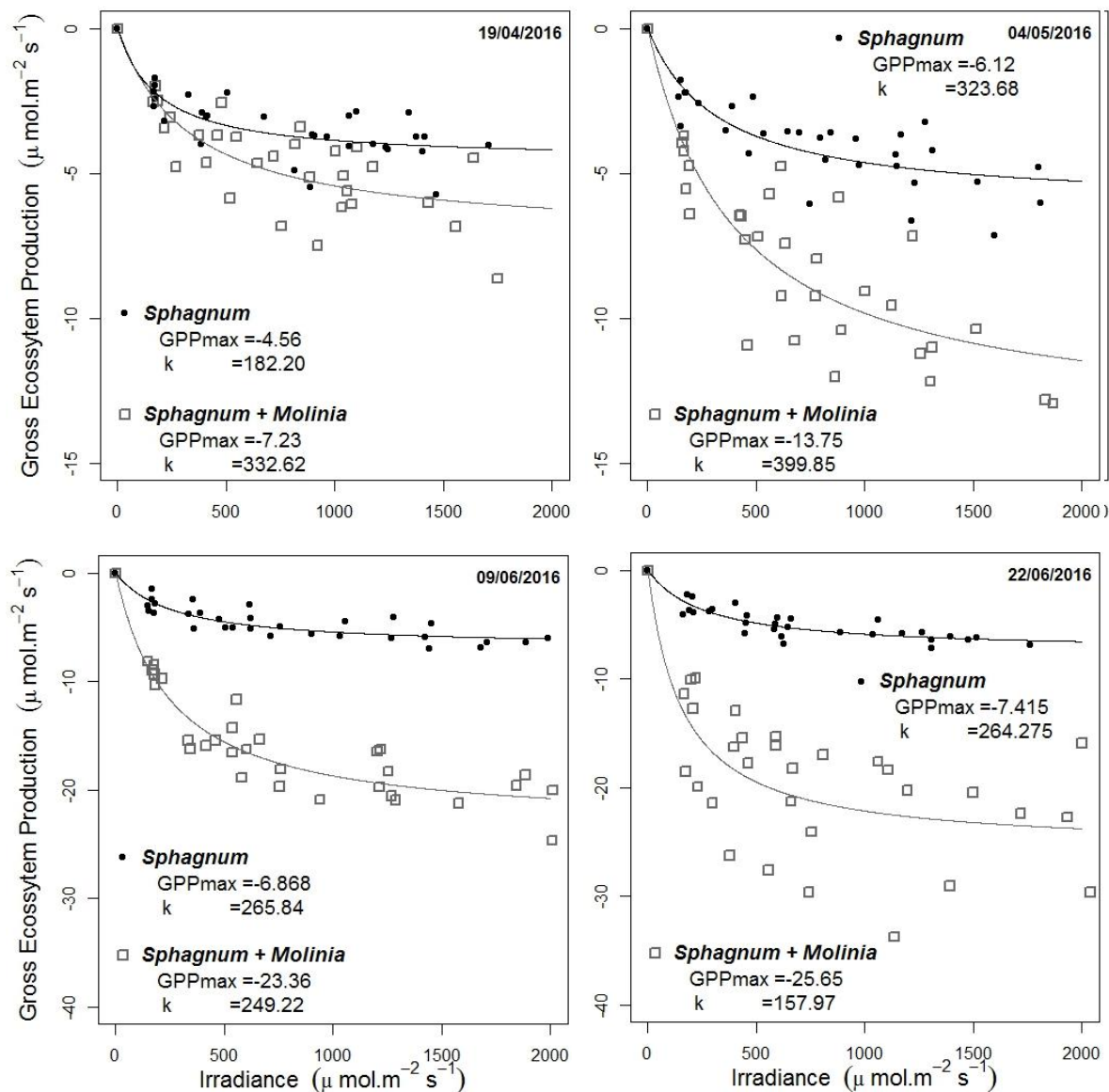


Figure 2: Dependence of gross primary production (GPP) on irradiance at four dates. The photosynthesis-irradiance curve shows the maximum rate of photosynthesis (GPP_{max}) and the half saturation value (k).

These increases are linked to *Sphagnum* growth and the number of *Molinia caerulea* leaves, respectively (Fig. 3). Based on these linear relationships, the GPP_{max} is variable in time depending on these vegetation indexes. The parameter k (μmol m⁻² s⁻¹, Eq. 4) is the half saturation value and was set at the mean k value of the four dates with a k equal to 259 μmol m⁻² s⁻¹ for *Sphagnum* plots and 285 μmol m⁻² s⁻¹ for *Sphagnum + Molinia* ones.

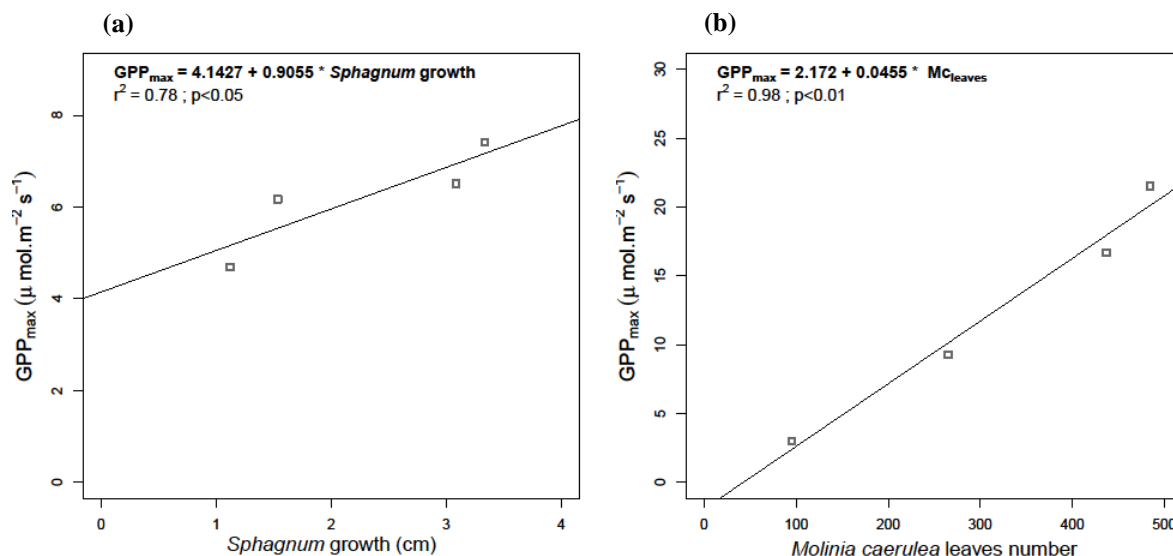


Figure 3: Linear relationship between the Gross Primary Production maximum (GPP_{max}) calculated with the photosynthesis-irradiance curve and *Sphagnum* growth (a) and the number of *Molinia caerulea* leaves (b).

Models validations were done using all the measurements points and showed a 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 emissions models

Calibration of the models showed a good agreement between the modelled and measured ER and CH₄ emissions with a high r^2 and low NRMSE for both plant communities (Table 2, Fig. 4a and 4d). 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. However, in *Sphagnum* + *Molinia* plots, the ER model validation showed a r^2 close to 0.6 but with the 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, Fig. 4c).

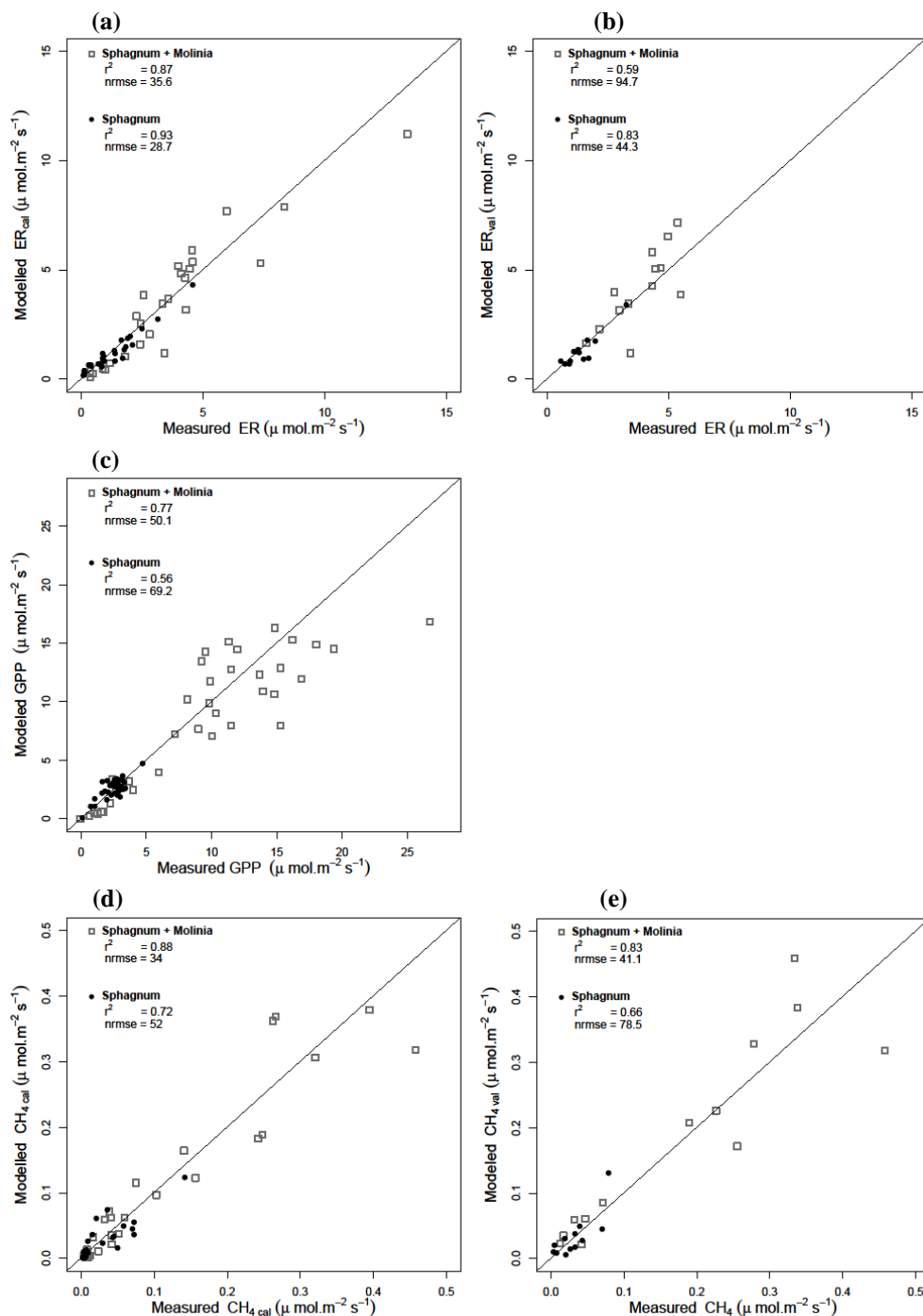


Figure 4: Calibration and validation of the models by comparison of simulated and measured ecosystem respiration (ER; a and b), gross primary production (GPP, c), and CH₄ emission (CH₄, d and e) in *Sphagnum* and *Sphagnum + Molinia* plots. The diagonal lines represent the 1:1.



- The model parameters a and c, respectively related to 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.
- 5 The f value, representing the temperature sensitivity, rose from 3.32 in *Sphagnum* plots to 5.08 in *Sphagnum + Molinia* plots.

Table 2: r², normalized root mean square errors (NRMSE) and adjusted model parameters for ecosystem respiration (ER), gross primary production (GPP), net ecosystem exchange (NEE) and CH₄ emissions (CH₄) in *Sphagnum + Molinia* and *Sphagnum* plots.

		Calibration		Validation	
		<i>Sphagnum</i>	<i>Sphagnum + Molinia</i>	<i>Sphagnum</i>	<i>Sphagnum + Molinia</i>
ER	r ²	0.93	0.87	0.82	0.59
	nrmse	28.7	35.6	46.8	94.7
	a	2.50	1.77	2.50	1.77
	b	0.33	0.0096	0.33	0.0096
	c	1.49	1.43	1.49	1.43
GPP	r ²	–	–	0.56	0.77
	nrmse	–	–	69.2	50.1
CH ₄	r ²	0.72	0.88	0.66	0.83
	nrmse	52	34	78.5	41.1
	d	0.041	-0.065	0.041	-0.065
	e	0.001	0.092	0.001	0.092
	f	3.32	5.08	3.32	5.08

3.5 Greenhouse gases carbon budget and global warming potential

- 10 The modeled annual GPP over the studied period represented an input of 414 gC m⁻² y⁻¹ in *Sphagnum* plots and of 1273 gC m⁻² y⁻¹ in *Sphagnum + Molinia* plots (Table 3). The ER and CH₄ emissions showed, respectively, an output of 376 and 7 gC m⁻² y⁻¹ in *Sphagnum* plots and of 1078 and 33 gC m⁻² y⁻¹ in *Sphagnum + Molinia* plots (Table 3).

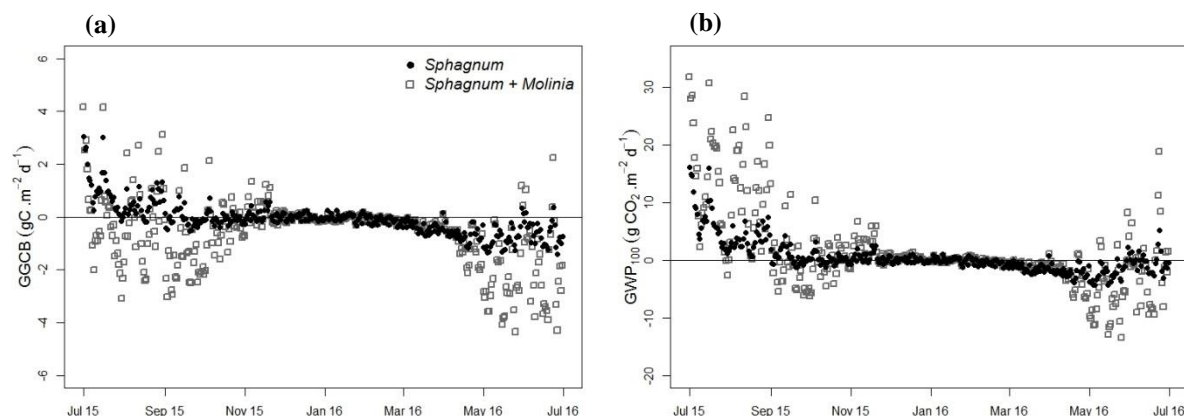


Figure 5: Greenhouse gases carbon budget (GGCB; a) and global warming potential over 100 years (GWP₁₀₀; b) average per day in *Sphagnum* and *Sphagnum + Molinia* plots.

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. 5a). In contrast, the GGCB in *Sphagnum + Molinia* plots was mostly negative with positive values only in October and November. The annual GGCB showed that *Sphagnum* plots absorbed 30 gC m⁻² y⁻¹ whereas the *Sphagnum + Molinia* plots absorbed 223 gC m⁻² y⁻¹ (Table 3). The GWP₁₀₀ for *Sphagnum* and *Sphagnum + Molinia* plots was, respectively, +195 and +547 g CO₂ eq m⁻² y⁻¹ (Table 3).

Table 3: Modeled annual gross primary production (GPP; gC m⁻² y⁻¹), ecosystem respiration (ER; gC m⁻² y⁻¹), net ecosystem exchange (NEE; gC m⁻² y⁻¹), CH₄ emissions (CH₄; gC m⁻² y⁻¹), greenhouse gases carbon budget (GGCB; gC m⁻² y⁻¹) and global warming potential over 100 years (GWP₁₀₀; g CO₂ eq m⁻² y⁻¹) in *Sphagnum + Molinia* and *Sphagnum* plots.

	GPP	ER	NEE	CH ₄	GGCB	GWP ₁₀₀
<i>Sphagnum</i>	-414	+ 376	-38	+ 7	-30	+ 195
<i>Sphagnum + Molinia</i>	-1273	+ 1018	-255	+ 33	-223	+ 547

By modulating the annual WTL and temperature, respectively from -2.5 to -9 cm and from 9.8 to 13.8°C, we observed a large variation of the GGCB from -400 to +300 gC m⁻² y⁻¹ (Fig. 6). By modelling an increase of temperature and a decrease of WTL, the GGCB increased in both plant communities (Fig. 6a and b), meaning more C loss, whereas high WTL and low temperature promoted high negative GGCB and thus more uptake of C in both plant communities. Increasing the temperature induced only a slight variation of the GGCB in *Sphagnum* plots but decreasing the WTL led to a larger modification (Fig. 6). In *Sphagnum + Molinia* plots, temperature and WTL seem to impact the GGCB equally. Under both vegetation covers, the increasing temperature or decreasing WTL increased the amplitude of GGCB variation under the other abiotic factor gradient.

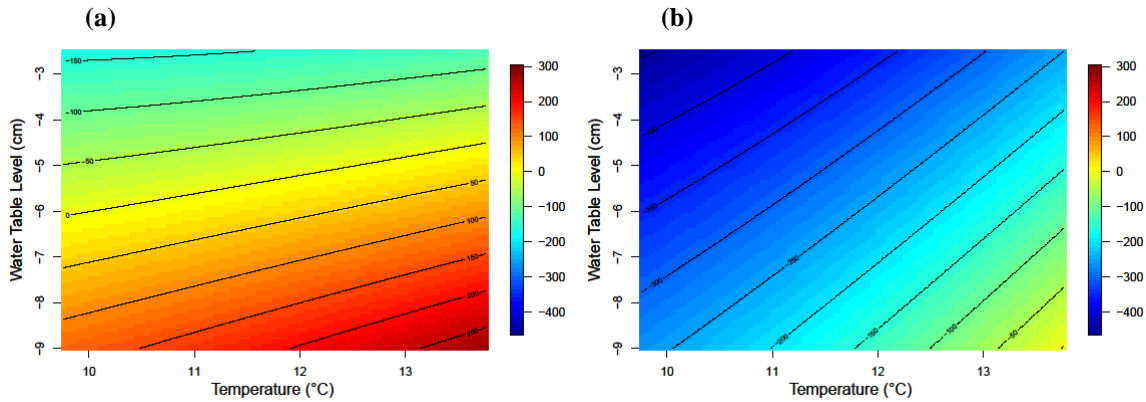


Figure 6: Modeled greenhouse gases carbon budget (GGCB, $\text{gC m}^{-2} \text{y}^{-1}$) for annual temperature average variation from 9.8 to 13.8°C and WTL fluctuation from 2.5 to -9 cm for *Sphagnum* (a) and *Sphagnum* + *Molinia* (b) plots.

For a hypothetical strong increase of 2 months in the length of the growing season, the NEE was more negative, from -21.3 to -26.7 $\text{mol CO}_2 \text{ m}^{-2} \text{y}^{-1}$ (Fig. 7). In comparison, an increase of two degrees in temperature caused a larger modification of NEE, from -21.3 to -10.7 $\text{mol CO}_2 \text{ m}^{-2} \text{y}^{-1}$ (Fig. 7).

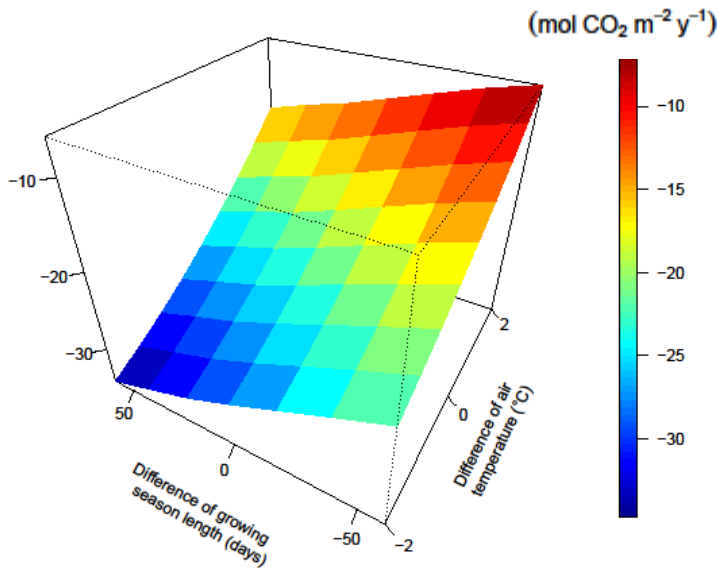


Figure 7: Modeled greenhouse gases carbon budget (NEE) with variations of the growing season length (-/+ 60 days) and air temperature (-/+ 2°C) for *Sphagnum* + *Molinia* plots



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 the latter, the GPP was higher with *Molinia caerulea*, with a C uptake close to $1300 \text{ gC m}^{-2} \text{ y}^{-1}$ against $400 \text{ gC m}^{-2} \text{ y}^{-1}$ with *Sphagnum* alone. The estimated GPP of *Sphagnum* mosses are consistent with studies conducted in boreal peatlands with a GPP close to $350 \text{ gC m}^{-2} \text{ y}^{-1}$ (Peichl et al., 2014; Trudeau et al., 2014). The GPP calculated with *Molinia caerulea* was higher than that measured in the site at La Guette peatland with an average of $1052 \text{ gC m}^{-2} \text{ yr}^{-1}$ (D'Angelo et al., in prep). Such a difference can be explained by the fact that in the field vegetation in collars contained other types of plants such as shrubs and woody chamephytes that exhibited 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 the simulation. Indeed, in comparison to *Sphagnum* mosses, vascular plants have an extensive root system which are 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), with half that can be mineralized into CO_2 in a week and promote the ER (Kuzyakov et al., 2001). 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 CO_2 emissions through decomposition. Higher CH_4 emissions with sedges compared to mosses or shrubs have been explained by the differences in root exudates quality and the aerenchyma of the sedges (e.g. Armstrong et al. 2015).

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 (Fig. 4). 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* govern it photosynthetic capacity and could further improve GPP models (Tuittila et al., 2004)

The ER models showed a similar sensitivity in both plant communities to abiotic factors with an empirical 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 aboveground and belowground respiration (Kandel et al., 2013). Modeling CH_4 as CO_2 emissions explained a good proportion of the variance (between 70 and 80%). The parameters of the CH_4 models differed with vegetation cover. Parameter d connected to the WTL had an opposite sign in the two vegetation covers. This difference was difficult to interpret as the large variation of parameter e shifted the relationship between parameter d and the WTL. Even so, the presence of *Molinia caerulea* increased the temperature sensitivity of CH_4 emissions. Such increase of the temperature sensitivity could result from modification of methanogenesis



pathways. Acetoclastic methanogenesis often dominated in minerotrophic peatlands, as La Guette peatland, and required less energy than hydrogenotrophic methanogenesis pathways (Beer and Blodau, 2007). Vascular plants, as *Molinia caerulea*, can influence the methane production through the introduction of roots exudates in the deep layer by providing substrate availability. Whilst roots exudates are source of acetate and thus suggested to favor acetoclastic methanogenesis (Saarnio et al., 2004), it can also stimulate the decomposition of recalcitrant organic matter favoring hydrogenotrophic methanogenesis (Hornibrook et al., 1997). Graminoids soils are colonized primarily by hydrogenotrophic methanogenesis (Kao-Kniffin et al., 2010) and shift from acetoclastic to hydrogenotrophic methanogenesis pathways could explain the increase of 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 consider in future studies.

4.3 Annual C fluxes and GGCB

The shift from *Sphagnum* to *Molinia*-dominated peat mesocosms increased the C fixation through the GPP that to lead to an increase of the annual C output with CO₂ and CH₄ emissions. The gaseous C balance shows that both plant communities act as C-sinks with a storage of 30 gC m⁻² y⁻¹ in *Sphagnum* plots and 223 gC m⁻² y⁻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. 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 y⁻¹, was produced with current-year photosynthates, meaning that the C-allocation in roots could account for 540 g C m⁻² y⁻¹. Such an amount corresponds to a larger proportion than the C stored in *Sphagnum* + *Molinia* plots (223 g C m⁻² y⁻¹) and could represent emission of the C already stored. Furthermore, C stored in roots, litters 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 GGCB predictions, by varying the temperature with the WTL and with the growing season length, revealed the sensitivities of the system to these three abiotic factors. Even if these predictions need to be treated with caution due to extrapolation outside the observed range of WTL and temperature, they showed the same trend in plots acting as a C-sink in the case of low temperature and high WTL and, on the contrary, as a C-source at high temperature and low WTL. More interestingly, they showed that increasing the temperature or decreasing the WTL makes the systems more sensitive to the other factor. Furthermore, a 2°C increase in temperature has a larger impact on NEE than a 2-month increase in the growing season.

The shift from *Sphagnum* 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 their potential role as a
5 substantial C source.

Author contribution.

FL, SG and FLD designed the experiment.

FL, SG, CG, XY, GB and WS collected data.

10 FL, SG, CG, LBJ and FLD performed model simulations and data analysis

FL prepared the manuscript with contributions from all co-authors

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