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Vegetation composition controls temperature sensitivity of CO₂ and CH₄ emissions and DOC concentration in peatlands

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Type of paper: Short Communication

Highlights

- The occurrence of *Molinia caerulea* increases CO₂ and CH₄ emissions in *Sphagnum*-dominated peat mesocosms.
- DOC concentration decreases with the presence of *Molinia caerulea* compared to *Sphagnum* with no *Molinia caerulea*.
- CO₂ and CH₄ emissions and DOC concentration are strongly related to soil temperature.
- Vegetation cover modifies the sensitivity of CO₂ and CH₄ emissions and DOC concentration to soil temperature.
- *Molinia caerulea* could affect the composition of the methanogenic communities.

Abstract

Plant community modification may play an important role in peatlands' carbon balance. We investigated how *Molinia caerulea* altered CO₂ and CH₄ fluxes and DOC concentration as well as their sensitivity to water table level, air and soil temperature in *Sphagnum*-dominated peat mesocosms. The presence of *Molinia caerulea* significantly increased CO₂ and CH₄ emissions compared to *Sphagnum* and decreased the DOC concentration. The rise in temperature exponentially increased DOC as well as CO₂ and CH₄ emissions. *Molinia caerulea* decreased the temperature sensitivity of CO₂ emissions, suggesting the presence of a more labile substrate (root exudates), while it increased the temperature sensitivity of CH₄ emissions, suggesting a possible change in methanogenic communities. Our study highlights a strong impact of vegetation change on C dynamics in peatlands.

Peatlands act as a global major carbon (C) store. They contain between 15 to 30% of the world soil C in only 3% of the global land area (Turunen et al., 2002; Gorham, 1991). The C-sink function of boreal peatlands results from particular environmental conditions (waterlogging, acidic soil and low temperature) and specific vegetation, i.e. *Sphagnum* mosses. However, global change is expected to modify plant species composition in northern *Sphagnum* peatlands, with an increase in vascular plants (e.g. graminoids) to the detriment of *Sphagnum* mosses (Dieleman et al., 2015; Buttler et al., 2015). Disturbed peatlands represent a large potential source of CO₂ and CH₄ to the atmosphere and of dissolved organic carbon (DOC) export to rivers (Limpens et al., 2008). Thus, understanding the feedback between vegetation change and C fluxes in peatlands is required to predict the future of the peatland C budget. The response of CO₂ and CH₄ emissions and DOC concentration ([DOC]) to abiotic control is well documented (Clark et al., 2009; Pypker et al., 2013). Nevertheless, studies on the sensitivity of C fluxes and [DOC] to abiotic factors in a context of vegetation change are lacking. Our aim was to assess to what extent CO₂ and CH₄ emissions and [DOC] sensitivities to abiotic factors in *Sphagnum* peat mesocosms could be modulated by the occurrence of vascular plants. The presence of graminoids in *Sphagnum* mesocosms is expected to change C fluxes through a more efficient C uptake that allocates C to the above- and belowground parts of the plant. Vascular plants have an extensive root systems, in comparison to *Sphagnum* rhizoids, able to exudate newly produced labile organic compounds (e.g. glucose; Saarnio et al., 2004; Fenner et al., 2007). According to Arrhenius function, the degradation rate of these compounds has a lower sensitivity to temperature than recalcitrant organic matter (Davidson and Janssens, 2006). Thus, *Sphagnum* peat mesocosms invaded by *Molinia caerulea* was sampled to investigate the three following hypotheses:

- (i) the presence of *Molinia caerulea* will increase the [DOC] due to a higher root exudate production compared to *Sphagnum* spp.,

- (ii) these labile exudates will be rapidly consumed by microbial communities and will enhance both CO₂ and CH₄ emissions,
- (iii) as the C source will be more labile, the sensitivity to temperature of the C fluxes will decrease compared to recalcitrant C (with higher activation energies).

Twelve peat mesocosms (depth and diameter: 30 cm) were collected in March 2015 in La Guette peatland (France). The studied site is an acidic fen invaded by *Molinia caerulea*, a graminoid plant invading numerous peatlands (Tomassen et al., 2003; Gogo et al., 2011). The mesocosms were buried outside and surrounded with a tarpaulin containing water from the peatland. Air and soil temperature at 5 and 20 cm depth were monitored in each mesocosm. The mesocosms were separated into 2 treatments: 6 containing only *Sphagnum rubellum* ('*Sphagnum*' cores) and 6 containing *Sphagnum rubellum* and *Molinia caerulea* ('*Molinia*' cores). *Molinia caerulea* started to grow in May and increased up to 60% of mesocosms on average until its senescence in November (see supplementary material).

Measurements were performed between two to eight times per month, from May 2015 to April 2016. Ecosystem Respiration (ER) was measured during 5 min using a closed chamber equipped with a GMP343 Vaisala (D'Angelo et al., 2016). CH₄ emissions were measured during 15 min using the SPIRIT, a portable infrared laser spectrometer (Guimbaud et al., 2011). Water table level (WTL) was manually measured in each mesocosm piezometer. Water was collected from the piezometer to measure [DOC] with a Shimadzu TOC-5000 analyzer. All measurements were performed in the same day and were related to WTL, air and soil temperature at 5 and 20 cm depth with exponential regression. R² from exponential regressions were calculated after a logarithmic transformation (linearization of the date). Temperature sensitivity was expressed through the temperature coefficient (Q₁₀; eq. 1), and energy of activation (E_a, eq. 2):

$$Q_{10}=(k_2/k_1)^{10/(T_2-T_1)} \quad \text{eq. 1}$$

k_1 and k_2 are rates at two observed temperatures T_1 and T_2 .

$$k=A.e^{(-E_a/RT)} \quad \text{eq. 2}$$

k is the reaction rate coefficient, A is the pre-exponential factor, R is the ideal gas constant and T is the temperature in Kelvin.

One-way ANOVAs with repeated measures were used to compare *Molinia* to *Sphagnum* cores.

Throughout the measurements, environmental conditions did not differ significantly between *Sphagnum* and *Molinia* cores other than the WTL which was 2.4 cm higher in *Sphagnum* cores than in the *Molinia* ones (Table I). WTL ranged from 2.5 cm to 17 cm (Fig 1a). Air temperature ranged from 0°C in January to 30°C in July (Fig 1b). Soil temperature at 5 and 20 cm depth varied from 2.3°C and 5°C in January to 27.3°C and 25.7°C in July, respectively (Fig 1c and 1d).

[DOC] were significantly lower in *Molinia* cores compared to *Sphagnum* ones (Table I, Fig 2c), which disproves our first hypothesis but supports the mechanisms proposed by Freeman et al. (2004) who suggested that labile DOC release, through root exudates, stimulates microbial activity and enhances the degradation of organic matter, in particular the DOC fraction. Mimics of roots exudates have been revealed to enhance microbial biomass in peat soil (Basiliko et al., 2012), that might, with *Molinia caerulea* occurrence, trigger a real priming effect leading to an increase of DOC consumption.

Furthermore, in contradiction to our third hypothesis, the presence of *Molinia* increased the [DOC] sensitivity to soil temperature (Q_{10} , E_a , Table II and Fig 2c). The Q_{10} values obtained were higher than those found by Freeman et al. (2001; $Q_{10}= 1.36$) but lower than those found by Clark et al. (2009; $Q_{10}= 1.84$ and 3.53 under anaerobic and aerobic conditions, respectively). As postulated by the latter authors, we showed that vegetation cover plays an important role in

the [DOC] and its sensitivity to soil temperature. Further studies on the DOC and vegetation relationship are essential to determine how vegetation change may alter this C pool.

CO₂ and CH₄ emissions were higher in the presence of *Molinia caerulea* comparing to *Sphagnum*, showing an average increase of 2.4 and 3.1 fold, respectively (Table I, Figure 2a and b). Similar observations have already been reported in peatlands with graminoids (e.g. Armstrong et al. 2015). The greatest CH₄ emissions were observed with *Molinia* occurrence, at the same time with an increase of the thickness of aerobic zone, which opposes with the general association of CH₄ emissions under anaerobic conditions. Such potential effect could be compensated with the fueling of methanogens in anaerobic peat by the root exudates, already related to the difference of CH₄ production among plants species (Koelbener et al., 2010). Furthermore, variations of CH₄ emissions are also controlled by the plant community and its ability to transport CH₄ (Schimel, 1995) and their potential for rhizospheric oxidation (Ström et al., 2005). If root exudates fuel the microbial communities, the C flux sensitivity to temperature is expected to decrease (Davidson and Janssens, 2006). This hypothesis was confirmed by the ER results: the presence of *Molinia* decreased the ER sensitivity to temperature (Table II). However, this did not hold for CH₄. The temperature sensitivity of CH₄ emissions increased in the *Molinia* cores (Table II). In natural systems, acetoclastic methanogens are dominant over hydrogenotrophic methanogens (Kao-Kniffin et al., 2010). However, as reported in the latter study, graminoid soils are colonized primarily by hydrogenotrophic metabolisms. These two methanogenesis pathways require different levels of energy: 195 kJ mol⁻¹ for hydrogenotrophic methanogenesis and 50 kJ mol⁻¹ for acetoclastic methanogenesis (Beer and Blodau, 2007). Thus the increased temperature sensitivity under *Molinia caerulea* could reflect the promotion of hydrogenotrophic communities.

ER, CH₄ emissions and [DOC] were correlated to WTL and soil temperature (Table II). Increased soil temperature enhanced exponentially these three C-fluxes under both plant

communities (Fig 2). Soil temperature explained the higher amount of variability compared to the WTL, even for CH₄ emissions. Such weak correlation with the WTL could also be due to the little WTL variation over the experiment. Our best fit between ER and temperature differed with the vegetation: ER in *Sphagnum* cores was more correlated to soil temperature at 5 cm, whereas with *Molinia caerulea* ER was more influenced by soil temperature at 20 cm (Table II; Figure 2a). *Sphagnum* photosynthesis occurs in the first centimeters of the peat profile, whereas root exudates excreted by *Molinia* could stimulate microbial activity deeper in the peat profile. These physiological differences between *Sphagnum* and *Molinia* may explain the best fit observed for ER and also for CH₄ emission and [DOC] (Table II).

In conclusion, both biotic (vegetation cover) and abiotic (mainly temperature) factors control CO₂ and CH₄ emissions and [DOC] in peat mesocosms. *Molinia caerulea* can deliver labile C stimulating microbial activity and promoting DOC consumption and CO₂ and CH₄ emissions. The increase in soil temperature enhanced [DOC] as well as CO₂ and CH₄ emissions. Moreover, our findings demonstrate that the two controlling factors interact and that vegetation modification changes the C-fluxes' sensitivities to temperature. Under global change, C-dynamics in peatlands are thus subjected to many alterations through plant community modification. This study advocates taking vegetation change into account in global models with a concomitant variation in the temperature sensitivity.

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Tables

Table I: Mean values of 12 months' measurements of Ecosystem Respiration (ER), CH₄ emissions (CH₄), Dissolved Organic Carbon (DOC), Water Table Level (WTL), photosynthetically active radiation (PAR) and air (Ta) and soil temperature (Ts) in *Molinia* and *Sphagnum* cores. Significance levels of one way ANOVAs with repeated measured are expressed as *p < 0.05, **p < 0.01, ***p < 0.001 (n = 6).

| | Mean | | <i>Molinia</i> / <i>Sphagnum</i> | P |
|---|----------------|-----------------|-------------------------------------|-----|
| | <i>Molinia</i> | <i>Sphagnum</i> | | |
| GHG fluxes | | | | |
| ER (μmol m ⁻² s ⁻¹) | 2.39 | 0.99 | 2.39 | *** |
| CH ₄ (μmol m ⁻² s ⁻¹) | 0.094 | 0.030 | 3.14 | * |
| Water compartment | | | | |
| DOC (mg L ⁻¹) | 31.9 | 55.7 | 0.57 | *** |
| WTL (cm) | -7.04 | -4.58 | 1.54 | *** |
| Environmental parameters | | | | |
| PAR (μmol m ⁻² s ⁻¹) | 711 | 741 | 0.96 | |
| Ta (°C) | 12.0 | 12.1 | 0.99 | |
| Ts at 5 cm (°C) | 13.1 | 13.1 | 1 | |
| Ts at 20 cm (°C) | 13.7 | 13.9 | 0.99 | |

Table II: Determination coefficient (r²) of exponential regressions for mean values of 12 months' measurements of Ecosystem Respiration (ER), CH₄ emissions (CH₄), Dissolved Organic Carbon (DOC) with Water Table Level, Air and Soil Temperature at 5 and 20 cm. Bold numbers represent the highest determination coefficient for each variable in *Sphagnum* and *Molinia* cores. Significance correlation are expressed as ^{-/+}p < 0.05, ^{-/+}++p < 0.01, ^{-/+}+++p < 0.001. ^{-/+} represents a negative or positive relationship, respectively.

| Variables | | Determination coefficient (r^2) | | Q_{10} | | Ea | |
|---------------------------|-----------------|--|---------------------------|-----------------|----------------|-----------------|----------------|
| | | <i>Sphagnum</i> | <i>Molinia</i> | <i>Sphagnum</i> | <i>Molinia</i> | <i>Sphagnum</i> | <i>Molinia</i> |
| | | | | | | | |
| Water Table Level | ER | 0.38 ⁻⁻⁻ | 0.23 ⁻⁻⁻ | | | | |
| | CH ₄ | 0.49 ⁻⁻⁻ | 0.18 ⁻ | | | | |
| | DOC | 0.12 ⁻ | 0.14 ⁻ | | | | |
| Air Temperature | ER | 0.72 ⁺⁺⁺ | 0.60 ⁺⁺⁺ | 3.75 | 2.58 | 92.2 | 65.7 |
| | CH ₄ | 0.00 | 0.01 | 1.00 | 1.01 | 2.3 | 4.7 |
| | DOC | 0.55 ⁺⁺⁺ | 0.46 ⁺⁺⁺ | 1.56 | 1.66 | 31.7 | 35.9 |
| Soil Temperature at 5 cm | ER | 0.76⁺⁺⁺ | 0.67⁺⁺⁺ | 4.09 | 2.86 | 97.6 | 72.9 |
| | CH ₄ | 0.68⁺⁺⁺ | 0.86⁺⁺⁺ | 5.61 | 7.61 | 119.4 | 140.2 |
| | DOC | 0.64⁺⁺⁺ | 0.60 ⁺⁺⁺ | 1.68 | 1.91 | 36.0 | 44.5 |
| Soil Temperature at 20 cm | ER | 0.65 ⁺⁺⁺ | 0.75⁺⁺⁺ | 4.01 | 3.38 | 97.3 | 85.0 |
| | CH ₄ | 0.59 ⁺⁺⁺ | 0.88⁺⁺⁺ | 4.05 | 9.13 | 94.6 | 153.1 |
| | DOC | 0.37 ⁺⁺⁺ | 0.70⁺⁺⁺ | 1.47 | 2.38 | 25.3 | 60.0 |

Figures

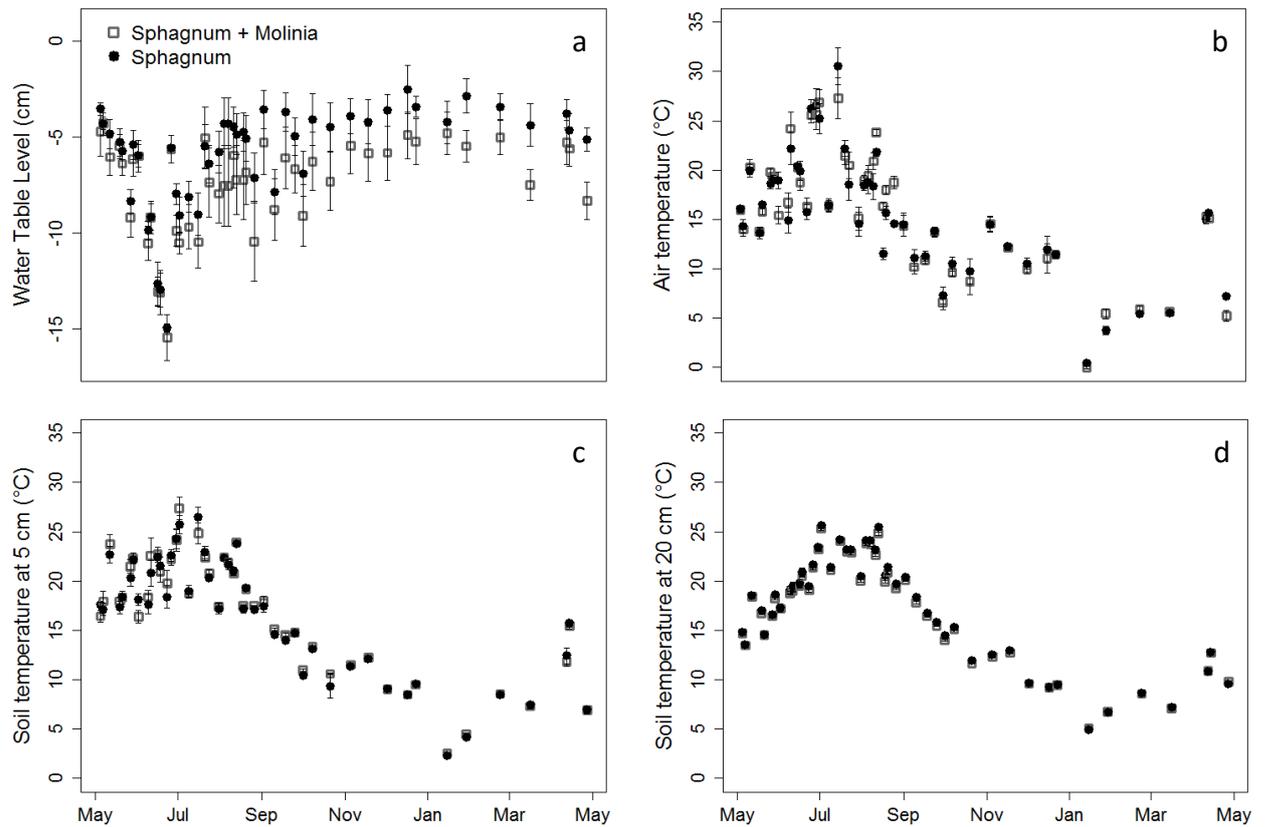


Figure 1: Time series of water table level (a), air (b) and soil temperature at 5 (c) and 20 cm (d) in *Sphagnum* and *Molinia* cores (\pm SE, $n=6$) from May 2015 to April 2016. Data were collected during greenhouse gas emission measurements.

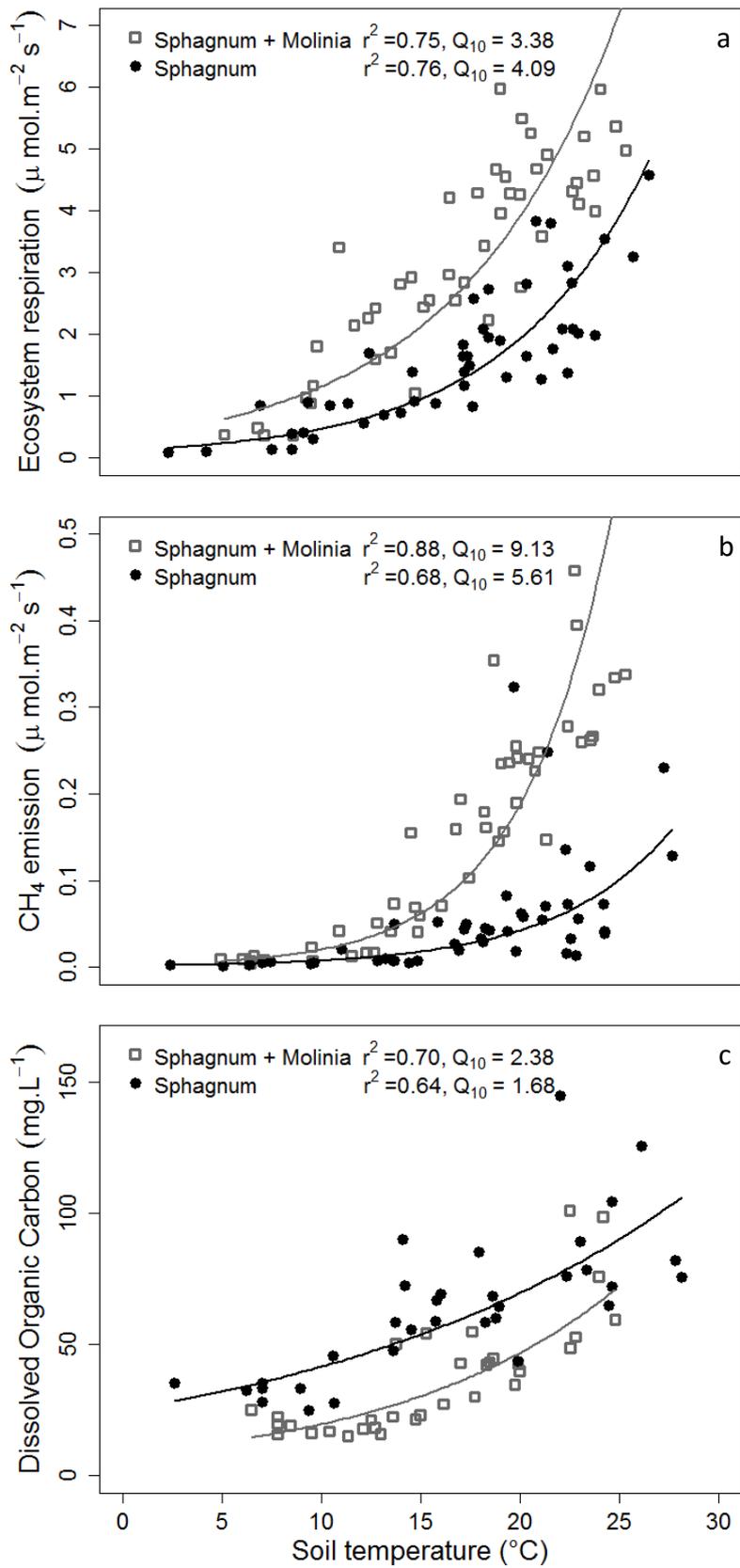


Figure 2: Exponential relationship between Ecosystem Respiration (a), CH_4 emission (b), Dissolved Organic Carbon (c) and soil temperature at 5 cm for *Sphagnum* cores and at 20 cm for *Molinia* cores

Supplementary materials

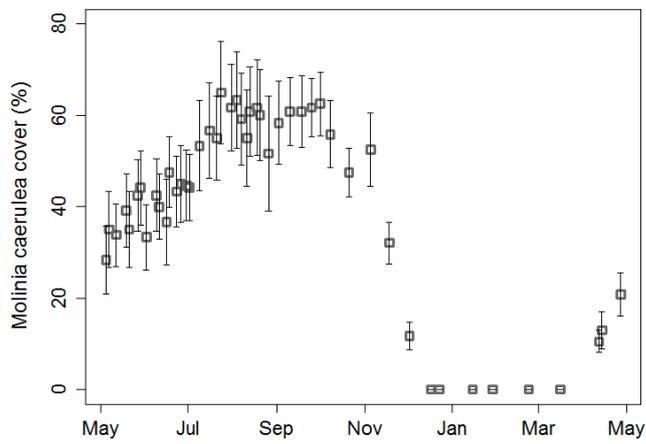


Figure 3: Time series of *Molinia caerulea* cover in *Molinia* cores (\pm SE, n=6) from May 2015 to April 2016. Data were collected during greenhouse gas emission measurements.