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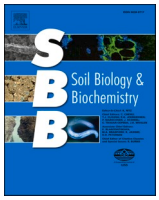

Short-term carbon cycling at a *Sphagnum* farming site under drought stress

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A B S T R A C T

Paludiculture is a new land use option for degraded peatlands, producing biomass under wet and peat preserving conditions. While previous studies indicate a significant greenhouse gas mitigation potential, the impact of bryophyte and vascular plant species on carbon cycling is not yet fully understood, especially under drought stress and climate warming conditions. In July 2018, we conducted a pulse labelling experiment at a *Sphagnum* farming area in Northwestern Germany to trace sequestered carbon dioxide ($^{13}CO_2$) in above-ground biomasses of peat mosses (*Sphagnum*) and dominant vascular plant species purple moor grass (*Molinia caerulea*), soil microbial biomass (C_{mic}), dissolved organic carbon (DOC), as well as dissolved and emitted CO_2 and methane under drought stress induced by summer drought and simulated climate warming using Open Top Chambers (OTCs). We observed fast label allocation to all investigated carbon pools with the exception of DOC. Although label uptake was clearly higher in *Molinia* compared to *Sphagnum*, most carbon was lost via respiration within a few days and the percentage of stored carbon after 140 days was clearly higher in *Sphagnum* and C_{mic}. Differences between warmed and control plots were small, presumably due to the already hot and dry conditions. Our results highlight that carbon uptake and storage processes are maintained even under extreme drought conditions, while further experimental warming using OTCs was less influential. The presented findings confirm the important role of *Sphagnum* in carbon retention and the risk of methane emissions even at low water levels via plant-mediated transport. Consequently, an elaborate irrigation management and control of vascular plants are the key to successful *Sphagnum* farming and GHG mitigation.

1. Introduction

Peatlands drained for agriculture and forestry release large amounts of carbon dioxide (CO_2) into the atmosphere (Leifeld and Menichetti, 2018). Paludiculture, which is the production of biomass under wet and peat preserving conditions in re-wetted peatlands aims at combining ecological and economic goals (Wichtmann et al., 2016). For ombrotrophic peatlands, peat mosses (*Sphagnum*) are the most promising paludiculture crop. Harvested *Sphagnum* can be used as substrate in horticulture (Emmel, 2008) or as donor material for peatland restoration (Quinty and Rochefort, 2003).

Due to their recalcitrant litter and the acidification of the surrounding environment, *Sphagnum* mosses play a key role in peat accumulation (Hobbie et al., 2000; Stivrins et al., 2017). However, the vegetation at *Sphagnum* farming sites is in a dynamic successional stage. Especially in the initial phase, this newly emerging ecosystem is highly vulnerable due to a not yet completely closed *Sphagnum* lawn. Vascular plants could intrude depending on site conditions and management. Under optimal conditions, gaps in the *Sphagnum* lawn close and abundances of vascular plants decrease. Still, *Sphagnum* mosses might be less competitive compared to vascular plants during droughts, as they possess no roots and rely on high and stable water levels (Buttler et al., 2015; Antala et al., 2022). For example, purple moor grass (*Molinia caerulea*) became dominant in some degraded peatlands in north-west Europe (Chambers et al., 2001), with possibly adverse effects on *Sphagnum* due to competition for light (Pilkington et al., 2021).

Greenhouse gas (GHG) balances of *Sphagnum* farming trials in Northwestern Germany indicate that these sites could quickly restore their function as sinks of atmospheric CO_2 under optimal conditions, i.e., high groundwater levels and little interference during the initial growth phase (Beyer and Höper, 2015; Günther et al., 2017; Oestmann et al., 2022a). While CO_2 emissions can generally be expected to decrease with rising water levels (Tiemeyer et al., 2020), methane (CH_4) emissions will increase (Abdalla et al., 2016; Evans et al., 2021), depending on management and vegetation (Wilson et al., 2009; Cooper et al., 2014). However, the longevity of CO_2 in the atmosphere makes a reduction of CO_2 emissions the most important goal of climate protection measures in peatlands (Günther et al., 2020). Nitrous oxide (N_2O) emissions might only play a larger role at poorly vegetated sites (Marushchak et al., 2011; Oestmann et al., 2022a).

The abundance of different plant functional groups affects short-term carbon (C) flux and GHG exchange (Ward et al., 2009; Gong et al., 2020). Vascular plants contribute substantially to C cycling processes (Crow and Wieder, 2005), although this impact depends on the respective process and the aggregation level of plant species and thus is difficult to be generalized (Dorrepaal, 2007). Altogether, they take up

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and allocate C faster compared to bryophytes and dead plant material is less recalcitrant to microbial decomposition. In addition, specialized vascular plants with aerenchymous tissues could enhance CH_4 emission even at low water level via plant-mediated transport of gases between rhizosphere and atmosphere (Oestmann et al., 2022b; Korrensalo et al., 2022).

As in the case of other ecosystems, the GHG balance of *Sphagnum* farming sites might be affected by climate change. Simulated climate warming conditions using Open Top Chambers (OTC) significantly increased GHG emissions at a near-natural bog and two *Sphagnum* farming areas in Northwestern Germany, governed rather by a decreased primary production than by increased ecosystem respiration, as well as by increased CH_4 emission due to higher abundances of aerenchymous vascular plants (Oestmann et al., 2022b).

More detailed information on C cycling at *Sphagnum* farming sites can be obtained from pulse labelling experiments using stable isotopes. Exposing plants to enriched CO_2 for a short time enables the tracing of sequestered C in plant biomass and subsequent C pools (Trinder et al., 2008; Studer et al., 2014). Trinder et al. (2008) were the first to apply this technique at an abandoned cutover peatland and found that three common vascular plant species (*Calluna vulgaris*, *Eriophorum angustifolium* and *Eriophorum vaginatum*) lost most of the assimilated label via shoot respiration and dissolved organic carbon (DOC), while root and peat respiration were small. For a subarctic tundra site, Street et al. (2013) demonstrated that *Sphagnum* increased ecosystem C use efficiency and retention, highlighting their important role in peat accumulation.

Despite the increasing importance of paludiculture for climate protection, the fate of plant assimilates and the longevity of the different C pools have not yet been closely followed. Understanding the contribution of different plant types to the allocation of fresh photosynthates is a prerequisite for developing adequate restoration measures and for optimizing *Sphagnum* farming. This is especially important during extreme events like droughts, which are expected to happen more frequently due to climate change (IPCC, 2021). In the present study, we are the first to address these questions for a paludiculture site using $^{13}CO_2$ pulse labelling.

The objective of this study was to shed light on the path of sequestered atmospheric C to the pools of bryophyte (*Sphagnum*) and vascular plant (*Molinia*) biomass, soil microbial biomass, dissolved C species in peat pore water and ecosystem respiration during the extreme event of the European heatwave 2018. In addition, the effect of simulated climate warming conditions on C allocation was investigated.

2. Materials and methods

2.1. Study area

The study area Provinzialmoor (52°40′ N, 07°06′ E) is a former industrial peat extraction site in Northwestern Germany, where the cultivation of peat mosses as a horticultural substrate (*Sphagnum farming*) is recently being tested. The climate is oceanic and average annual air temperature and precipitation are 9.8 °C and 791 mm, respectively (1971–2000, Lingen, German Climate Service). However, in 2018, 11.7 °C and only 561 mm were measured, as the European heatwave 2018 led to an extraordinary hot and dry summer and autumn. A more detailed site description and GHG balances are given in Oestmann et al. (2022a), while the effect of experimental passive warming on the GHG exchange over two years (March 2017 to March 2019) is described in Oestmann et al. (2022b). In brief, experimental warming increased CH_4 emissions in the study area. The overall increase in CO_2 emissions was masked by the cover of vascular plants, which was lower in the warmed plots in comparison to the control plots in the first measurement year (2017) and higher in the second (2018). This resulted in an increased gross primary production at the warmed plots in 2018, while R_{eco} was hardly affected.

The labelling experiment reported in the present study took place at the warmed ("P-MIX-W") and control ("P-MIX") sites of the warming experiment. Both sites consisted of three replicate plots (0.75 m × 0.75 m), which were randomly distributed along boardwalks in distances of about two to 3 m. In each plot, *Sphagnum* and *Molinia* grew in different abundances (Table 2). Passive warming was achieved using permanent hexagonal Open Top Chambers (OTC; 0.5 m height and 2.1 m chamber base width; Molau and Mølgaard, 1996), which were constructed from transparent polycarbonate (Makrolon 3 mm, 87% light transmittance, Bayer AG, Darmstadt, Germany) and increased air and soil temperatures by 0.5 ± 0.9 °C and 0.3 ± 0.4 °C (averaged over two years, Oestmann et al., 2022b).

After peat extraction ceased in 2008, the area was re-wetted as a shallowly flooded polder. In 2015, the water table was lowered and in October 2016, a large-scale *Sphagnum* farming field trial was established by the moss layer transfer technique (Quinty and Rochefort, 2003). Moss fragments quickly developed into new moss plants and in 2018, the area was almost completely (>80%) covered by a *Sphagnum* lawn (mainly *Sphagnum papillosum* LINDB.) with scattered vascular plants (mainly *Molinia caerulea* L., as well as some *Eriophorum angustifolium* HONCK. and *Erica tetralix* L.). The site was irrigated via shallow ditches connected to several adjacent polders, designed to store excess winter precipitation for dry summer months. The highly decomposed peat layer had a thickness of about 0.8 m and was classified as Ombric Hemic Histosol (IUSS Working Group WRB, 2015).

2.2. Environmental conditions and vegetation survey

At each plot, air (0.20 m) and soil temperatures (−0.02 m) were recorded in half-hourly intervals. Water table depths (WTD) were measured at the warmed and control site using Mini-Divers in perforated dip wells close to the measurement plots and Baro-Divers for atmospheric pressure correction (Eijkelkamp, Giesbeek, The Netherlands). A nearby meteorological station (distance approximately 100 m) recorded air and soil temperatures and photosynthetically active radiation (PAR).

Covers of *Sphagnum* and *Molinia caerulea* were estimated using the Londo scale (Londo, 1976) every six months. Here, we use the data of September 2018, when additionally C contents of selected *Sphagnum* plants and *Molinia* leaves were measured by elemental analysis (LECO Corporation, St. Joseph, Michigan, USA). Further, leaf area index (LAI) and plant biomass dry weight (DW) were determined for *Sphagnum* and *Molinia* according to Wilson et al. (2007). First, total numbers of *Sphagnum* capitula and *Molinia* leaves were counted in 25 random sub-sample parcels (0.10 m × 0.10 m) per plot and extrapolated to the total plot area. For *Sphagnum*, leaf and stem areas of ten plants were determined by scanning. These values were extrapolated to the plot area using the total number of capitula per plot and the plot area to derive LAI ($m^2\ m^{-2}$). For *Molinia* LAI, leaves were divided into seven size classes to account for the different individual leaf area per size class, scanned and extrapolated to the plot area. Mean DW were obtained by weighing 20 moss plants and 127 *Molinia* leaves (divided in 7 size classes) and extrapolating to plot area by multiplying with the total number of plants or leaves per plot. Below-ground biomasses could not be determined due to ongoing GHG measurements.

2.3. Pulse labelling

On July 19th, 2018, i.e., approximately one and a half year after the installation of OTCs, all six plots were exposed to enriched carbon dioxide ($^{13}CO_2$, 99 at%, Sigma-Aldrich, Taufkirchen, Germany) for 5 h using transparent polycarbonate chambers (0.78 m × 0.78 m × 0.50 m). In a preliminary test, it was ensured that PAR was only slightly reduced by raised water vapor levels and that the temperature inside the chamber did not exceed a critical level of 40 °C. During labelling, CO_2 concentration inside the chambers was continuously monitored (LI-820, LI-COR, Lincoln, Nebraska, USA). $^{13}CO_2$ was injected (50 ml $^{13}CO_2$) into

the chamber head space using three-way stopcocks and gas-tight syringes when concentrations fell below 350 ppm. As, despite all management efforts, WTDs fell far below optimum conditions for *Sphagnum* growth (partly >0.40 m below soil surface) due to the ongoing drought, plant C sequestration was lower than expected. Consequently, CO_2 concentrations in the chamber head space continuously rose to more than 1000 ppm in the second half of the labelling procedure. Thus, label was added approximately every half hour, in total 500 ml $^{13}CO_2$ per plot, which equals 0.265 g^{13}C. This high amount of label was regarded sufficient to guarantee an uptake by both bryophytes and vascular plants given a mean daily gross primary production of 3.3 g CO_2–C m^{-2} in July 2018.

2.4. Tracing of enriched carbon in the investigated carbon pools

The C isotopic ratios of plant above-ground biomass, ecosystem respiration (R_{eco}), emitted methane (CH_4), soil microbial biomass (C_{mic}), as well as dissolved organic carbon (DOC) and dissolved gases (CO_2 and CH_4) in 10 cm and 30 cm depths were measured before label addition (day −1), 3 h (day 0) and 1, 2, 3, 5, 7, 10, 14 and 21 days after label addition (short-term C turnover), as well as 140 days thereafter (mid-term storage of incorporated C). These sampling dates were chosen as the key period of short-term C turnover during which photosynthate is allocated to growth or respiration is about three weeks (Street et al., 2013; Kritzler et al., 2016). Between the end of labelling and the first sampling (day 0), plots were left to aerate for 3 h, to allow back diffusion of label from soil pores and plant interspace before the start of measurements. Sampling was always conducted at the same time of the day and plant biomass and peat were sampled at the end of each campaign. The disturbance of vegetation cover and soil surface was minimal, as only small amounts of plant biomass (about 0.1 g dry mass per sample) and peat (about 12 g dry mass per plot) were needed for analyses. Carbon isotopic signatures ($^{13}C/^{12}C$) of samples measured via isotopic ratio mass spectrometry (IRMS) were expressed using the delta notation ($\delta^{13}C$, ‰), i.e., by comparison to the reference standard (V-PDB).

Two to four single *Sphagnum* plants were sampled randomly from the plot area using tweezers and were further divided into the green living capitula (SPH_{Cap}, the upper 1 cm) and the remaining, less active parts (SPH_{Rem}). In addition, two to three leaves of *Molinia* (MOL) were cut. In December (day 140), MOL leaves were mostly dead and brown. All plant material was stored frozen until further analysis. In the laboratory, it was dried at 105 °C, ground in a ball mill and C isotopic compositions were measured from homogenized material using IRMS (Delta Plus, Thermo Fisher Scientific, Waltham, MA, USA).

For R_{eco} analysis, head space air was sampled from opaque white PVC chambers (0.78 m × 0.78 m × 0.50 m) into exetainers (Labco Ltd., Lampeter, UK) directly after placing the chambers and every 20 min thereafter (t_0, t_{20}, t_{40}, t_{60}, t_{80}). Directly after each CO_2 exetainer, 100 ml glass vials were filled for determining isotopic ratios of emitted CH_4. The C isotopic compositions of CO_2 and CH_4 as well as concentrations of CO_2 were determined at the Centre for Stable Isotope Research and Analysis of the University of Göttingen (KOSI) using IRMS (Delta plus XP, Thermo Fisher Scientific, Bremen, Germany). CH_4 concentrations were later measured from the same exetainers using a gas chromatograph (Shimadzu, Kyoto, Japan) equipped with a flame ionization detector. Isotopic signatures of R_{eco} and emitted CH_4 at the moment of sampling were determined as Keeling plot intercepts of the linear regression of the isotopic composition on the respective inverse value of gas concentration of the five consecutive head space samples (Pataki et al., 2003). In the case of CO_2, regressions with $R^2 < 0.9$ were discarded from further analyses. However, minimum R^2 was set to 0.75 at campaign day 140 (early December) due to low fluxes. For CH_4, minimum R^2 of the Keeling intercepts was set to 0.75 and two intercept values below −100‰ were additionally discarded.

Soil pore water samples were extracted from 10 cm to 30 cm depths using borosilicate glass suction plates (pore size about 1 µm; ecoTech GmbH, Bonn, Germany; connected via Teflon tubes). Subsamples for the measurement of DOC concentrations were stored cool until analysis (DimaTOC, 2000; Dimatec, Essen, Germany). The remaining water was stored frozen and later freeze dried to measure the isotopic composition of DOC using IRMS (Delta Plus). Due to the dry conditions, soil pore water accumulated slowly and the sampled amounts are assumed to represent the water accumulation during the preceding day. Some samples could not be taken at all. Before reaching glass collection bottles, the sampled soil pore water passed a glass vial inside the collection bottle closed with a gas-tight septum via an inlet and an outlet needle. Those were adjusted in such a way that about 9 ml of the 22 ml vial volume were filled with water. From these vials, dissolved CO_2 and CH_4 were extracted by overhead shaking until equilibrium (1 h), extracting 1 ml from the head space air to evacuated and nitrogen flushed exetainers using a gas-tight syringe (SGE, Trajan Scientific, Ringwood, Australia) and measuring isotopic ratios of CO_2 and CH_4 at the KOSI.

For soil microbial biomass, moist peat samples of about 60–80 g (upper 0.10 m) were taken using a cut off syringe and stored frozen. Before further analyses, samples were preincubated for 24 h at 8 °C and 12 h at 15 °C. Subsequently, larger roots were removed with tweezers and samples were roughly homogenized by hand. Extractable soil microbial biomass was determined by chloroform fumigation extraction (CFE), following the protocol of Vance et al. (1987), modified by Helfrich et al. (2008). For each peat sample, the water content of a subsample of about 5 g was determined overnight. The next day, the remaining peat was split in six subsamples, all corresponding to 2 g dry weight. Three of them were fumigated for 24 h using ethanol-free chloroform. The non-fumigated peat samples were diluted in 40 ml 0.05 M K_2SO_4, shaken for 1 h and filtered (8–12 µm, Sartorius, Göttingen, Germany). We used a higher dilution of K_2SO_4 than proposed by Vance et al. (1987) in order to prevent bias of isotopic analyses by salt load. The fumigated samples were treated as the non-fumigated at the next day. Finally, concentrations of organic C in the filtrate were determined (DimaTOC, 2000) and the remaining filtrate freeze-dried for ^{13}C analysis. Carbon contents per gram of dry soil of the fumigated and non-fumigated samples were calculated as follows:

$$\mu g\ C\ g^{-1}\ DS = \mu g\ C\ ml^{-1} \times (40\ ml + WC) / DS \quad [1]$$

where WC is the water content of sample (ml) and DS is the amount of dry soil (g). Extractable soil microbial biomass (C_{mic}, µg C per g dry soil) was calculated by subtracting the C contents of the non-fumigated samples from the fumigated samples. No correction factor for determining the exact amount of microbial biomass from extracted C amounts was applied due to the high uncertainty of this factor for organic soils (Joergensen, 1996; Helfrich et al., 2008). Therefore, we use the term extractable soil microbial biomass and stress that values cannot easily be compared with literature but are considered sufficient to compare warmed and control plots. Isotopic signatures of C_{mic} were calculated as:

$$\delta^{13}C_{mic} = (\delta^{13}C_F * C_F - \delta^{13}C_{NF} * C_{NF}) / C_{mic} \quad [2]$$

where δ^{13}C and C are the isotopic signatures and C contents (µg C per g dry soil) of the fumigated and non-fumigated filtrates, respectively (Helfrich et al., 2008).

2.5. Isotopic signatures and mass balance calculations

For mass balance calculations, isotopic ratios were derived from δ^{13}C values and transformed to ^{13}C atom% values (abundances). Finally, ^{13}C abundances (atom%) before label addition ("day −1") were subtracted from each sample and C pool to derive excess ^{13}C abundances (atom% excess).

The quantity of ^{13}C fixed during label addition by *Sphagnum* and *Molinia* plants was calculated by multiplying peak ^{13}C atom% excess values of plant biomass with the respective biomass in each plot (determined in September 2018) and average C contents of 44.2%,

42.6% and 45.1% for MOL, SPH_{Cap} and SPH_{Rem}. Accordingly, the amount of ^{13}C stored in plant and microbial biomass at day 140 was calculated and given as percentage of the initially fixed amount for MOL, SPH_{Cap}, SPH_{Rem} and C_{mic}.

Losses of fixed ^{13}C via R_{eco} were calculated by multiplying ^{13}C atom % excess values with the corresponding daily R_{eco} fluxes (g CO_2–C m^{-2} d^{-1}; Oestmann et al., 2022b) and summing up daily amounts. Gaps in isotopic ratios at days between sampling dates were filled by linear interpolation. Daily R_{eco} values were derived from monthly measurement campaigns using opaque chambers. The Lloyd Taylor function (Lloyd and Taylor, 1994) was fit to soil temperature and R_{eco} of each campaign. Time series were then interpolated by applying these functions to half-hourly soil temperature data (Oestmann et al., 2022b). Fluxes of CH_4 were determined for each campaign day from the five consecutive CH_4 concentrations using the calculation procedure described in Oestmann et al. (2022a). Daily CH_4 fluxes between campaign days were derived from linear interpolation.

2.6. Statistical analyses

Data analysis was conducted using R software (R Core Team, 2021). Differences in isotopic ratios of each C pool and site measured before labelling and at the end of the experiment were investigated using paired t-tests. For differences between two C pools or treatments (warmed, control) at a respective campaign day, Wilcoxon rank sum tests were used.

Further, we used linear mixed effect modelling (package "nlme", Pinheiro et al., 2021) to investigate differences between time series of air and soil temperatures (hourly measurements) as well as of isotopic ratios of investigated C pools (campaign days) at warmed and control plots on a significance level of the likelihood ratio test of 0.05 (Zuur et al., 2009). For each comparison, a full model with treatment (warmed, control) as fixed factor and measurement plot as random factor was compared to a "zero" model, where treatment was replaced by the overall mean. In both models, an autocorrelation structure of order 1 was applied, as well as a power variance function structure if it improved the model as indicated by a lower AIC value.

3. Results

3.1. Environmental conditions

The environmental conditions during the experiment were extraordinary hot and dry. Especially during the first 21 days, precipitation amounts were low, while temperatures were high (Fig. 1, Table 1). Only towards the end of the experiment, higher precipitation led to more favorable conditions for *Sphagnum* growth.

The already high air and soil temperatures were even increased in the warmed plots during all considered time spans of the experiment (Table 1) and this increase was more pronounced during daytime (PAR

Table 1
Air and soil temperatures (°C) of the warmed and control plots (means and standard deviations of hourly measurements) during the experiment (study period from 19th July 2018 to 6th December 2018). $T_{Air,\ Day}$ refers to daytime air temperatures (PAR >0). Superscript letters a and b indicate statistical significances of each comparison between warmed and control plots.

Time period	Site	T_{Air}	$T_{Air,\ Day}$	T_{Soil}
First 7 days	Warmed	25.9 ± 8.7^a	30.3 ± 7.2^a	23.4 ± 3.7^a
	Control	25.1 ± 7.9^b	28.9 ± 6.6^a	22.9 ± 3.7^a
First 21 days	Warmed	24.6 ± 9.1^a	29.6 ± 7.0^a	22.7 ± 3.6^a
	Control	23.6 ± 8.4^b	28.2 ± 6.4^b	22.2 ± 3.7^a
Study period	Warmed	14.1 ± 9.4^a	19.7 ± 9.2^a	13.7 ± 6.4^a
	Control	13.6 ± 8.9^b	18.7 ± 8.7^b	13.5 ± 6.4^a

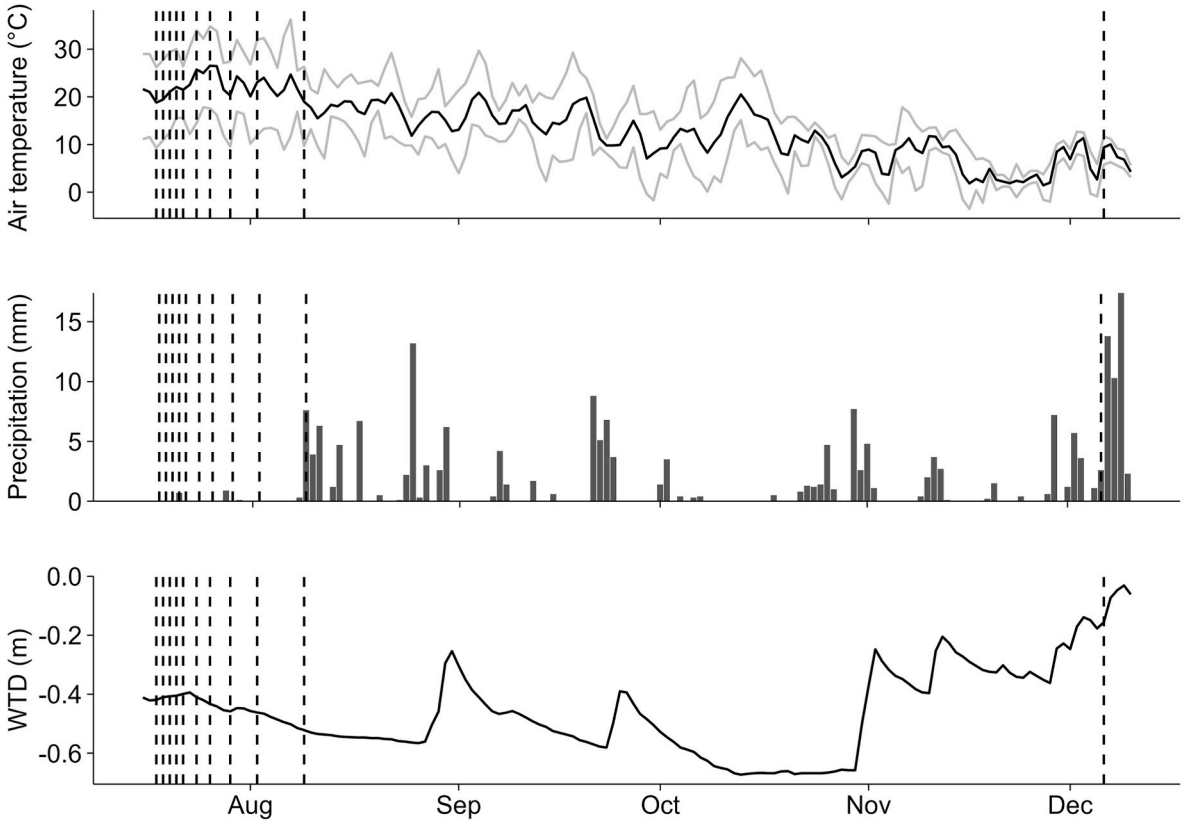

Fig. 1. Air temperature at the meteorological station (daily mean, minimum and maximum), precipitation (5 km distance to study area, German Climate Service) and daily mean water table depths (WTD) at the control site in 2018. The vertical dashed lines denote the sampling dates.

Table 2
Leaf area index (LAI, $m^2\ m^{-2}$) and dry weight (DW, $g\ m^{-2}$) of *Sphagnum* (SPH) and *Molinia caerulea* (MOL) at the warmed and control site in September 2018 (means and standard errors of the three replicate plots).

Site	LAI_{SPH}	LAI_{MOL}	DW_{SPH}	DW_{MOL}
Warmed	4.2 ± 0.4	0.1 ± 0.1	149.0 ± 14.1	12.5 ± 7.8
Control	4.7 ± 0.6	0.4 ± 0.2	166.7 ± 20.5	58.2 ± 25.2

>0), when photosynthesis takes place. In contrast to air temperature, the increase in soil temperature was not significant. During the first 21 days, mean daily WTDs at the control site were 0.45 ± 0.04 m below soil surface, in December it was 0.09 ± 0.05 m. In particular, the upper peat layer dried out during summer.

3.2. Vegetation

In September 2018, mean (±SE) covers of *Sphagnum* sp., total vascular plants and *Molinia caerulea* in particular were 81 ± 0%, 15 ± 3% and 7 ± 5% at the warmed and 77 ± 3%, 12 ± 3% and 7 ± 2% at the control plots, while in the preceding vegetation survey (March 2018), *Molinia* cover had been lower in the warmed plots than in the control plots (6 ± 5% and 10 ± 4%). Mean leaf area index (LAI) and mean dry weight (DW) of *Sphagnum* was higher compared to MOL (Table 2). In contrast to mean covers, LAI_{MOL} and DW_{MOL}, as well as LAI_{SPH} and DW_{SPH}, were clearly lower in the warmed plots.

3.3. Carbon fluxes

In the first 21 days, daily R_{eco} fluxes ranged between 3.7 and 4.9 g C m^{-2} with negligible differences between warmed and control plots. At the end of the experiment, they were lower than 1 g C m^{-2}. In comparison to R_{eco}, CH_4 fluxes contributed only minorly to overall C fluxes (Table 3). Cumulative sums of daily R_{eco} and CH_4 fluxes at the warmed and control plots from July to December did barely differ (R_{eco}: 373 and 356 g C m^{-2}; CH_4: 0.9 and 0.7 g C m^{-2}).

Concentrations of DOC in the soil pore water ranged between 37 and 141 mg l^{-1}. They were higher in the upper peat horizon (10 cm) than in 30 cm depth in the first days of the experiment. Extractable soil microbial biomass (C_{mic}) was within a range of 200–1300 μg g^{-1} dry soil. The amounts varied between sampling campaigns from relatively low amounts end of July and early August (on average 320 μg) to higher amounts at days 21 and 140 (>1000 μg). Amounts of DOC and C_{mic} did not clearly differ between warmed and control plots.

Table 3
Mean (±SD) interpolated daily R_{eco} fluxes ($g\ C\ m^{-2}$) and daily CH_4 fluxes ($mg\ C\ m^{-2}$) as well as mean (±SD) concentrations of dissolved organic carbon (DOC; $mg\ l^{-1}$) in 10 and 30 cm depth and extractable microbial biomass (C_{mic}; μg g^{-1} dry soil) during measurement campaigns (n = number of samples per treatment and period). Several DOC values are missing due to dry conditions.

		R_{eco}	CH_4	DOC_{10}	DOC_{30}	C_{mic}
First 7 days	Warmed	4.7 ± 0.1[a] (n = 7)	11 ± 0[a] (n = 7)	106 ± 29[a] (n = 3)	79 ± 16[a] (n = 3)	358 ± 40[a] (n = 5)
	Control	4.8 ± 0.1[a] (n = 7)	7 ± 1[b] (n = 7)	113 ± 18[a] (n = 3)	80 ± 2[a] (n = 3)	363 ± 87[a] (n = 5)
First 21 days	Warmed	4.4 ± 0.3[a] (n = 21)	11 ± 1[a] (n = 21)	75 ± 37[a] (n = 5)	81 ± 12[a] (n = 5)	407 ± 237[a] (n = 8)
	Control	4.5 ± 0.3[a] (n = 21)	7 ± 1[b] (n = 21)	86 ± 31[a] (n = 5)	80 ± 2[a] (n = 5)	424 ± 255[a] (n = 8)
Study period	Warmed	2.6 ± 1.2[a] (n = 140)	6 ± 2[a] (n = 140)	72 ± 34[a] (n = 6)	77 ± 14[a] (n = 6)	516 ± 365[a] (n = 9)
	Control	2.5 ± 1.2[a] (n = 140)	5 ± 1[b] (n = 140)	79 ± 30[a] (n = 6)	75 ± 11[a] (n = 6)	528 ± 363[a] (n = 9)

3.4. Pattern of label uptake and allocation

Before label addition (day −1), the mean (±SE) C isotopic signatures of *Sphagnum* and *Molinia* above-ground biomass of all plots was −27.2 ± 0.4‰ and −28.9 ± 0.2‰, respectively. Signatures of DOC and C_{mic} were −25.5 ± 0.2‰ and −23.4 ± 0.2‰, of R_{eco} and CH_4 they were −27.3 ± 0.2‰ and −79.8 ± 4.4‰. In 10 cm depth, signatures of dissolved CO_2 and CH_4 were −22.7 ± 0.1‰ and −30.3 ± 1.1‰, in 30 cm depth −18.4 ± 0.7‰ and −54.5 ± 10.3‰.

Samples of MOL leaves were highly enriched directly after labelling. In contrast, SPH_{Cap} and SPH_{Rem} showed low ^{13}C uptake with indistinct peaks distributed between 3 h and five days after label addition (Fig. 2). SPH_{Cap} was more enriched than SPH_{Rem}, although the temporal pattern of label concentration in both plant compartments was similar. The mean quantities of MOL and SPH (capitulum and remaining parts combined) label uptake at the control site were 56 ± 39 mg ^{13}C and 8 ± 1 mg ^{13}C, at the warmed plots it was 14 ± 13 mg ^{13}C and 7 ± 2 mg ^{13}C. The higher uptake of MOL at the control plots is a result of much higher LAI and DW (Table 2). In fact, the isotopic enrichment of MOL was higher in the warmed plots.

The concentration of ^{13}C in MOL leaves declined exponentially to about 25% of the initially taken up amount during the first three days and to about 10% in two weeks. In contrast, the decline in SPH ^{13}C enrichment was slow.

The highest R_{eco} ^{13}C abundance was measured 3 h after label addition. Similar to the pattern of MOL biomass, the ^{13}C values declined exponentially for about three weeks, although the enrichment was less than 10% of the peak value already at day 5. During the first 21 days, about 0.14 g ^{13}C was lost as R_{eco} per plot, which is slightly more than half of the applied label. The emitted CH_4 was also enriched in ^{13}C shortly after label addition, although far less than R_{eco}. Unfortunately, 27 of 66 CH_4 isotopic signatures are missing as the Keeling plots did not meet the required quality criterion ($R^2 < 0.75$).

The label reached the soil microbial community (C_{mic}) of the upper peat layer approximately two days after label addition. Label concentration remained relatively low and stable until it dropped to near pre-labelling conditions at days 21 and 140.

The allocation of label to DOC was negligible (Fig. 3). However, the enrichment of dissolved CO_2 in 10 cm depth roughly followed above-ground patterns with high peaks in the first three days after label addition, while in 30 cm depth, the peak was far less pronounced. Isotopic signatures of dissolved CH_4 in 10 cm and 30 cm depth differed clearly from the signatures of emitted CH_4. In 30 cm depth, a distinct enrichment is visible during the first days after label addition, while enrichment in 10 cm depth showed no clear pattern.

3.5. Effect of passive warming

At the warmed plots, SPH_{Cap} and SPH_{Rem} were less enriched compared to the control plots and MOL was more enriched, although differences between replicate plots were high (Fig. 4). MOL enrichment is in contrast to the smaller MOL ^{13}C uptake in the warmed plots resulting from the lower MOL biomass. While R_{eco} ^{13}C signatures did not differ between treatments, CH_4 fluxes were slightly more enriched at the warmed plots and C_{mic} clearly less. As shown by mixed effects modelling, differences between time series of isotopic ratios of warmed and control plots were only significant for MOL ($p < 0.05$) and C_{mic} ($p < 0.001$). In the case of SPH, this could be the result of the high variability between sampling days and replicates, while CH_4 could not be tested due to the high number of missing values.

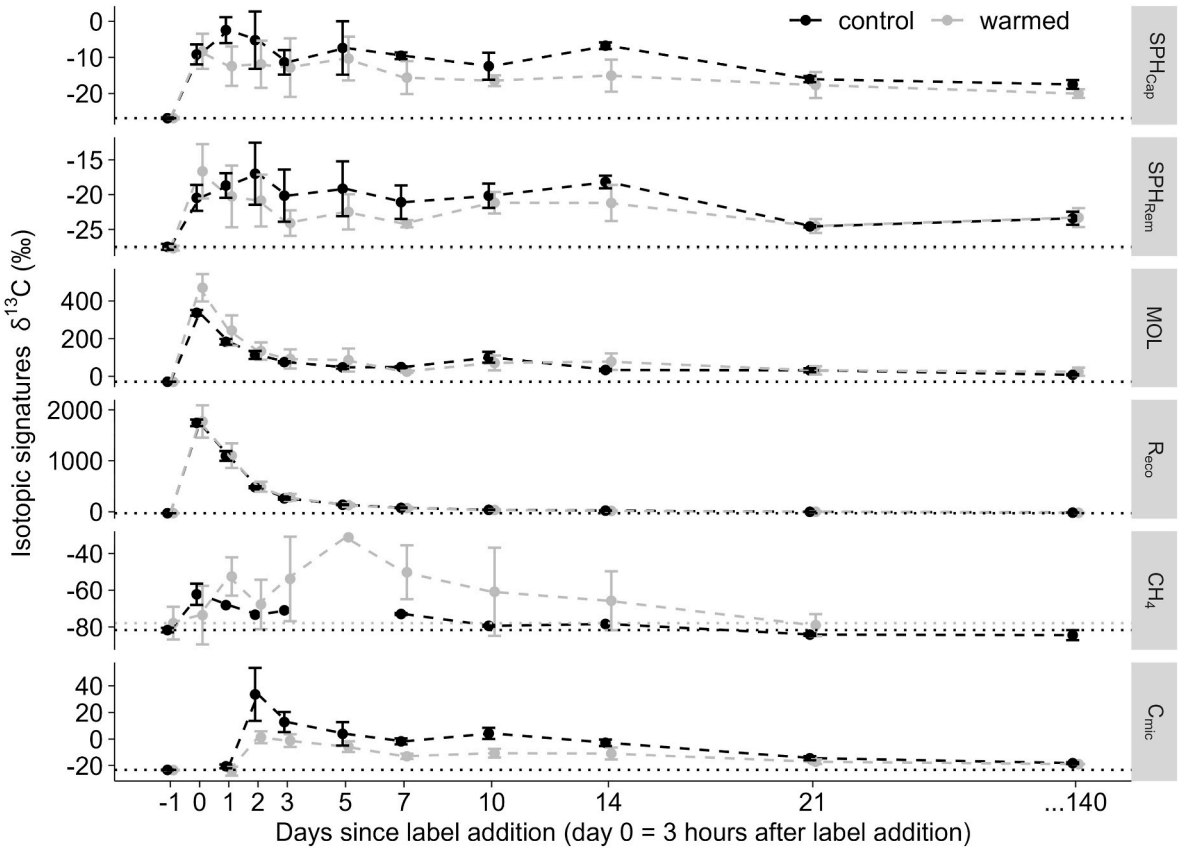

Fig. 2. Time series of isotopic signatures (means and standard errors of the three replicate plots) of the carbon pools *Sphagnum* capitulum (SPH_{Cap}), *Sphagnum* remaining parts (SPH_{Rem}), *Molinia caerulea* (MOL), ecosystem respiration (R_{eco}), emitted methane (CH_4) and extractable soil microbial biomass (C_{mic}). Dotted lines denote the pre-labelling („day −1“) signatures. Day 0 is the sampling directly after label addition (3 h). Note the time interval between sampling days 21 and 140.

The slightly higher enrichment of DOC in the warmed plots is more likely a result of missing replicate samples due to low WTDs. Dissolved gases in 10 cm depth could not be compared for the same reason. In 30 cm depth, dissolved CO_2 tended to be more enriched at the warmed plots and dissolved CH_4 slightly less (Fig. 3).

3.6. Label recovery at the end of the experiment

At the end of the experiment (day 140), MOL, SPH_{Cap}, SPH_{Rem}, R_{eco}, and C_{mic} were still significantly enriched compared to pre-labelling conditions (p-value < 0.01). Differences between warmed and control plots were not significant. Methane ratios could not be compared due to missing values.

Assuming a relatively constant biomass over the time course of the experiment, 33 ± 6%, 35 ± 4% and 10 ± 2% of the fixed ^{13}C (peak enrichment) was still incorporated in SPH_{Cap}, SPH_{Rem} and MOL leaves at day 140, respectively (Fig. 5). When considering the higher C_{mic} amounts at campaign day 140 compared to the campaigns of peak ^{13}C enrichment (on average 464 and 1267 μg per g dry soil), label recovery in C_{mic} was 53 ± 5% and 33 ± 19% at the warmed and control plots.

4. Discussion

4.1. Label uptake and allocation

Our results shed light on C allocation in *Sphagnum* farming under drought and heat stress (European heatwave 2018 plus passive warming). Label uptake by *Sphagnum* (SPH), which temporarily became visibly pale and inactive, was low compared to the uptake by *Molinia caerulea* (MOL). Possessing roots, *Molinia* was able to connect to deeper peat layers with higher moisture and assimilated substantial amounts of $^{13}CO_2$ despite drought conditions. Highest ^{13}C uptake in graminoid leaf tissue and low uptake by bryophytes were also reported in a plant removal study of Ward et al. (2009). However, under controlled laboratory conditions and constant high water levels, Fenner et al. (2004) found considerably higher label uptake in *Sphagnum* capitula, which underlines the severe impact of drought on *Sphagnum* metabolism at our sites. The stable SPH enrichment during the first three weeks in contrast to the exponential decline in MOL might hint towards reassimilation of respired pulse-derived CO_2 (Fenner et al., 2004; Turetsky and Wieder, 1999) or more likely to the allocation of label to more recalcitrant pools. The higher enrichment of SPH_{Cap} compared to SPH_{Rem} fits to the decreasing photosynthesis from *Sphagnum* capitulum to lower parts (Fenner et al., 2004).

A large share of assimilated label was lost via respiration within days. Although the experimental design did not allow for a separation of autotrophic and heterotrophic respiration and the exact contribution of SPH and MOL to R_{eco} remains unknown, the comparison of time series of isotopic ratios clearly indicates a relation of R_{eco} and MOL. It has to be noted here that further plant species in the measurement plots contributed to R_{eco}. Although there might have additionally been back diffusion of label from soil pore spaces during the first hours (Fenner et al., 2004; Subke et al., 2009), this should have been minimized by the aeration of plots after label addition.

Ecosystem respiration is majorly affected by drought conditions, which are complex. At very low moisture contents, plant respiration is reduced (Street et al., 2013). While light droughts increase heterotrophic respiration (Kritzler et al., 2016), severe droughts will additionally reduce microbial growth and activity due to lack of water (Mäkiranta et al., 2009; Moyano et al., 2013). This was also probably the case at our

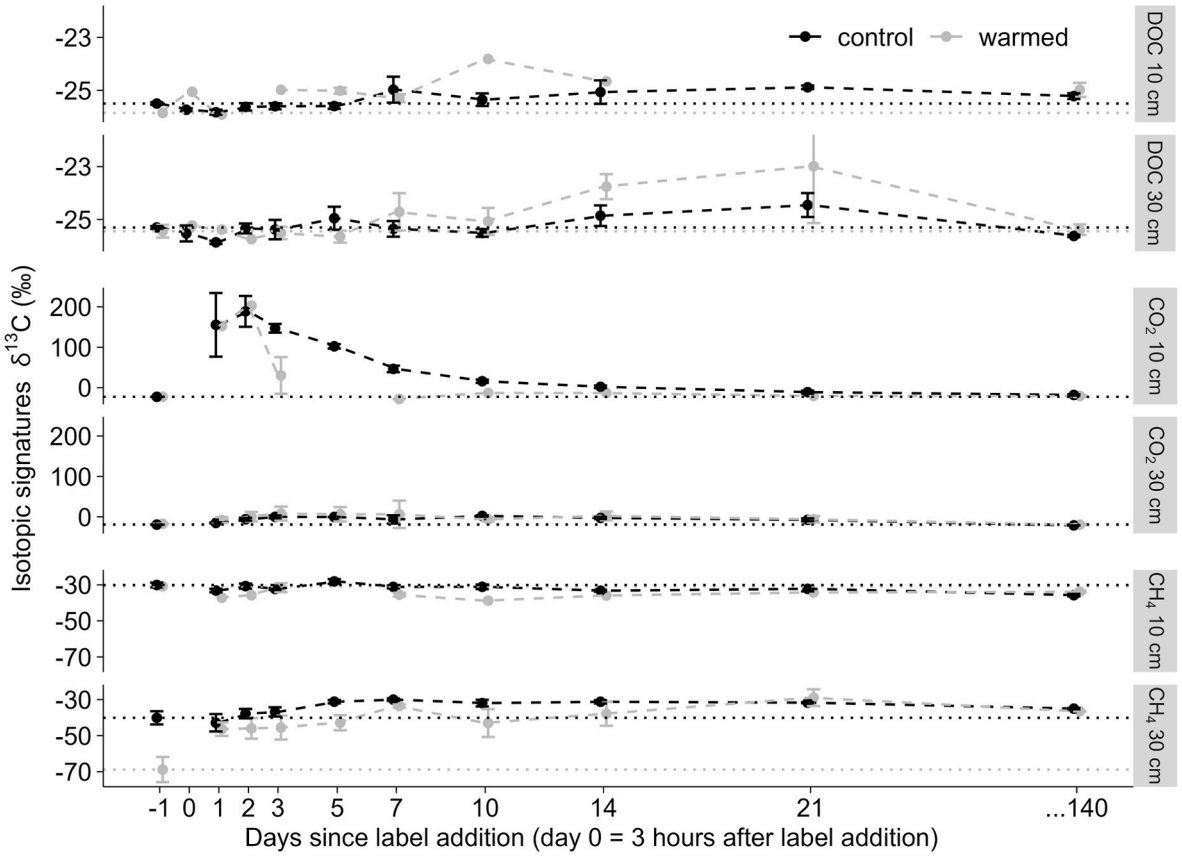

Fig. 3. Time series of isotopic signatures (means and standard errors of the three replicate plots) of dissolved organic carbon (DOC), dissolved carbon dioxide (CO_2) and dissolved methane (CH_4) in soil pore water at depths of 10 cm and 30 cm. Dotted lines denote the pre-labelling („day −1“) signatures. Day 0 is the sampling directly after label addition (3 h). Note the time interval between sampling days 21 and 140.

site as C_{mic} increased towards the end when conditions became wetter.

The allocation of label to methanogenesis was low compared to R_{eco} and the results are difficult to interpret due to the high number of missing values and due to the wide range of C isotope ratios in wetland CH_4, resulting from isotope fractionation by methanogens of 20–60‰ (Shoemaker and Schrag, 2010). Hornibrook (2009) reports ratios from −100‰ for CH_4 emitted via aerenchymous transport to −42‰ and higher for dissolved CH_4 remaining after preferential loss of $^{12}CH_4$, which roughly fits to the pre-labelling ratios of dissolved and emitted CH_4 in our study. However, uncertainty in discussing the isotopic ratios of dissolved gases might arise from the fact that the described sampling procedure is novel and lacking comparative studies. In particular, the depletion of pre-labelling ratios of dissolved CH_4 seems to be very low.

Unger et al. (2021) found at a restored temperate fen that the 2018 European drought negatively affected methanogen abundance and increased methanotroph abundance. The relatively fast allocation of C to CH_4 emission within hours is therefore surprising but not implausible as plant-derived C can be converted rapidly to CH_4 (King et al., 2002). The increasing enrichment of dissolved CH_4 in 30 cm depth indicates ongoing methanogenesis in deeper peat layers. The enrichment of emitted CH_4 further hints towards the important role of plant-mediated CH_4 transport during drought (White et al., 2023). As *Molinia* was the dominant vascular plant during the experiment, we chose this species for analyses, but there were other vascular species such as *Eriophorum* in some plots. The plot with the highest *Eriophorum* cover (*E. vaginatum* + *E. angustifolium*) showed highest CH_4 fluxes and highest CH_4 enrichment, at the other plots this relation was inconsistent. In contrast to previous studies (Leroy et al., 2019), *Molinia* seemed to have no effect on CH_4, indicated by higher CH_4 emission and enrichment at the warmed plots despite lower mean LAI.

The production of DOC was obviously decoupled from C allocation in the present study. Above-ground plant biomass and soil microbial biomass were significantly enriched after labelling, but DOC was not. This contrast to similar studies (King et al., 2002; Fenner et al., 2004; Trinder et al., 2008) could possibly be explained by the high and stable water level in these studies. However, the most obvious explanation is that bulk DOC at our site is originating from peat mineralization rather than plant derived C. The study site was characterized by a high degree of peat decomposition, which is known to result in high DOC concentrations (Frank et al., 2014) which might result in low amounts of fresh (and labelled) plant exudates being invisible. Further, ^{14}C studies have shown that DOC of highly decomposed peat is “old” compared to DOC in more natural sites and thus not necessarily dominated by recent input (Hulatt et al., 2014; Kalbitz et al., 2000). In contrast to DOC, the enrichment of dissolved CO_2 in 10 cm depth was significant. Peak enrichment in dissolved CO_2 was earlier than in C_{mic}, pointing towards root respiration as main source at least in the first hours while the possible diffusion of label into soil during labelling needs to be also considered. The much less enriched dissolved CO_2 in 30 cm depth might be a result of a low rooting density.

The label reached the microbial biomass of the upper peat layer (C_{mic}) with a delay of about two days. Enrichment remained relatively stable during the first two weeks. The enrichment of C_{mic} is in contrast to the missing enrichment of DOC and might be the result of diffusive flow of label into the soil (Zeh et al., 2021), plant-mediated transport of enriched CO_2 or small amounts of rapidly metabolized plant exudates (Tavi et al., 2013), which were not captured in DOC.

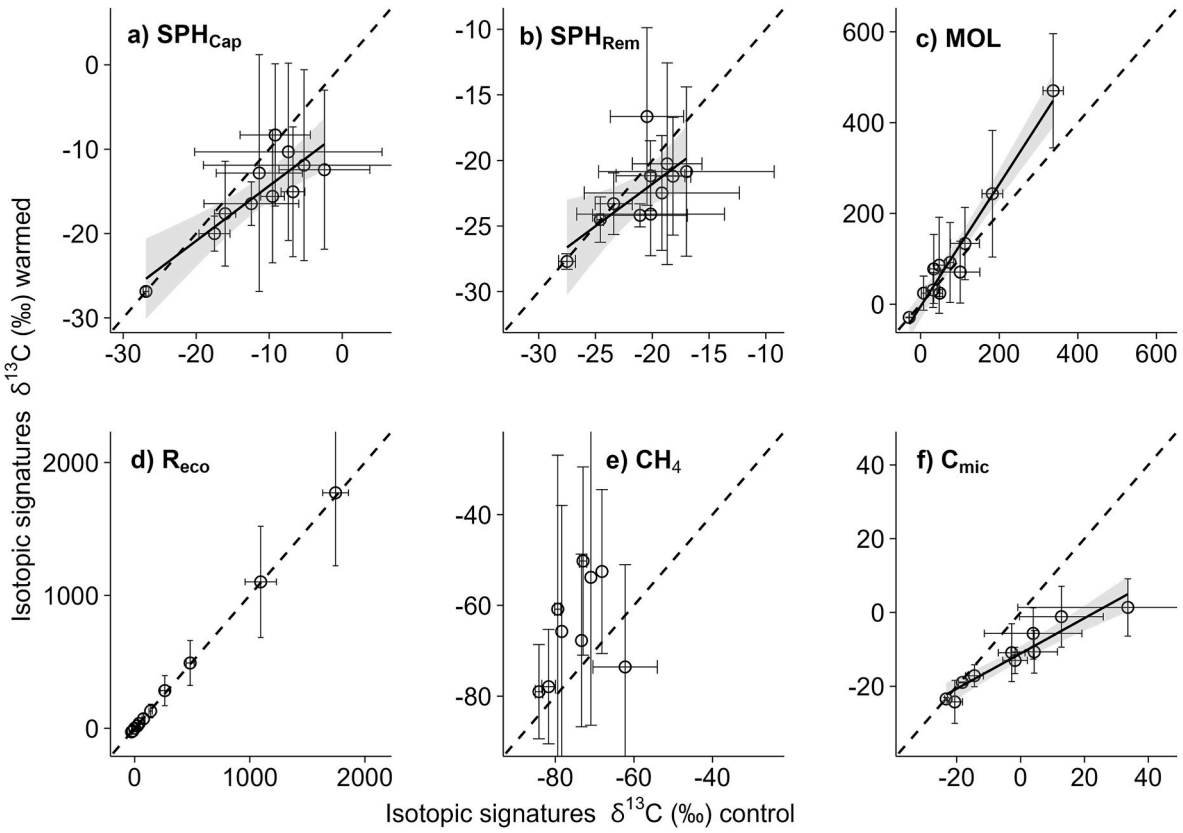

Fig. 4. Isotopic signatures (means and standard errors) of warmed and control plots for a) *Sphagnum* capitula (SPH_{Cap}), b) *Sphagnum* remaining parts (SPH_{Rem}), c) *Molinia caerulea* leaves (MOL), d) ecosystem respiration (R_{eco}), e) emitted methane (CH_4) and f) extractable soil microbial biomass (C_{mic}). The dashed lines denote the 1:1 ratio while the solid lines at SPH, MOL and C_{mic} represent a linear regression (confidence interval = 0.95).

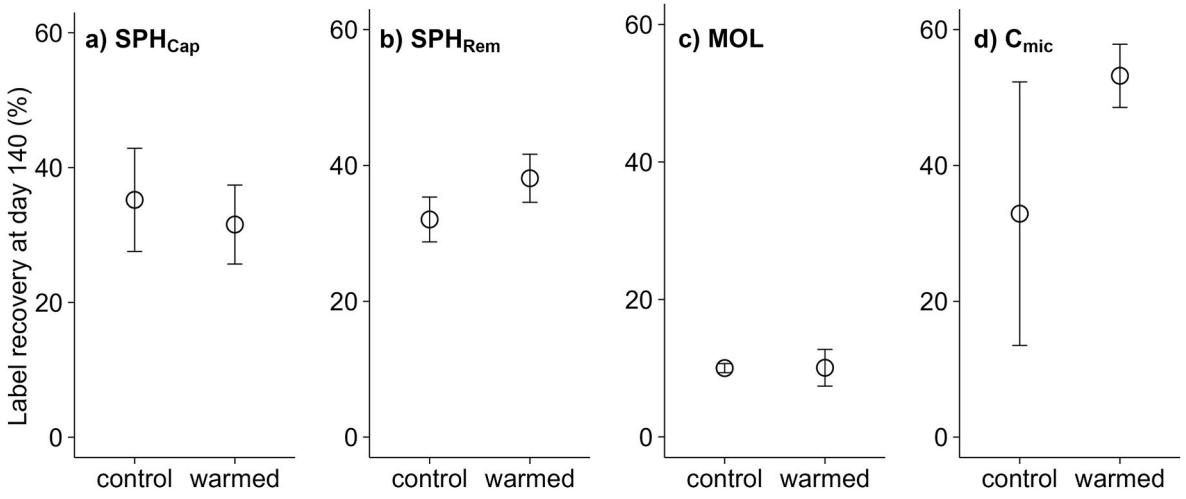

Fig. 5. Label recovery (means and standard errors of the three replicate plots) at the end of the experiment as percentage of the initial ^{13}C uptake for a) *Sphagnum* capitula (SPH_{Cap}), b) *Sphagnum* remaining parts (SPH_{Rem}), c) *Molinia caerulea* leaves (MOL) and d) extractable soil microbial biomass (C_{mic}).

4.2. Impact of warming on carbon allocation

When discussing the warming effect, it has to be considered that passive warming via OTCs started one and a half year prior to the labelling experiment (in March 2017) with possible medium-term effects on C cycling processes. Still, the effect of warming on C allocation and storage was rather marginal despite distinct differences in air and soil temperatures. This might be due to the already extraordinary hot and dry conditions in 2018 and the interaction of temperature and soil moisture, i.e., warming effects might have been more pronounced under optimum moisture conditions (Aerts, 2006; Mäkiranta et al., 2009).

The higher enrichment of MOL at the warmed plots in contrast to the lower enrichment of SPH underlines the higher competitivity of *Molinia* during drought and climate warming conditions. Although the special micro environmental conditions created by the OTC panels, i.e., shelter from excess wind, might have additionally affected plant activity, the results highlight that future warming and prolonged dry periods could increase the abundance of vascular plants (Munir et al., 2015) possibly

at the expense of reduced *Sphagnum* (Norby et al., 2019).

The warming experiment described in Oestmann et al. (2022b) revealed that warming did not affect or even slightly decreased annual R_{eco} sums at the study area. However, the warming effect was interwoven with ongoing vegetation succession and prolonged dry periods. In addition, the present study found no significant impact of warming on C isotopic ratios of R_{eco} despite slightly higher covers of total vegetation and vascular plants.

Warming might increase CH_4 emission at degraded peatlands even during dry periods (Oestmann et al., 2022b), presumably via plant-mediated transport from the rooting zone to the atmosphere (Dorodnikov et al., 2011). This mechanism could also be the reason for the higher CH_4 enrichment at the warmed plots, as mean covers of vascular plants and *Eriophorum* in particular were slightly higher here.

The lower ^{13}C allocation to C_{mic} at the warmed plots could be a result of the lower amounts of assimilated ^{13}C by MOL and SPH and also fits to the lower enrichment of dissolved CO_2 in 10 cm depth. In addition, Zeh et al. (2021) report that higher temperatures can decrease the path of fresh plant assimilates into the soil due to lower root biomass or reduced belowground allocation.

4.3. Longevity of carbon pools

A smaller fraction of applied ^{13}C was incorporated into more stable biomass products. When discussing the high percentage of retained C in C_{mic}, the much lower soil microbial biomass during the first days compared to the end of the experiment has to be considered. However, similar values have been reported for a wide range of biomes (Qiao et al., 2019).

The fast C turnover in MOL as indicated by the high label uptake and subsequent exponential decay is in contrast to the slower turnover and long residence time of sequestered C in SPH. Unfortunately, belowground biomass of MOL could not be determined due to ongoing measurements. *Molinia* develops deep roots and bulbous internodes, which might have also stored sequestered label or translocated it to C_{mic}. Peat mosses nevertheless stand out by the high percentage of fixed C after 140 days, which highlights their important function as ecosystem engineers also at degraded peatlands with a missing functioning acrotelm. Although previous studies (Fenner et al., 2004; Street et al., 2013; Woodin et al., 2009) report higher values under more favorable conditions, our results underline the resilience of *Sphagnum* C retention even under drought and heat stress.

4.4. Implications for future Sphagnum farming

Altogether, the results of the present study illustrate the need to closely monitor restoration attempts and paludiculture sites with respect to the complex impacts of climate warming. In order to maximize its potential, *Sphagnum* farming as a newly emerging land use option and ecosystem will have to cope with heat events and irregular precipitation. Insufficient water supply will trigger adverse effects, increasing the risk of higher vascular plant abundance (Mäkiranta et al., 2017) and possibly reducing C sink strength (Woodin et al., 2009). However, the recreation of the peat moss lawn half a year after the European heatwave 2018 indicates that *Sphagnum* farming is resilient against extreme climate events to a certain degree. Our results further highlight, that C uptake and storage processes are maintained even under these extreme conditions.

CRediT authorship contribution statement

Jan Oestmann: Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Arndt Piayda:** Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Dominik Düvel:** Investigation, Methodology, Writing – review & editing. **Bärbel Tiemeyer:** Conceptualization, Investigation, Methodology, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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