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RESEARCH ARTICLE

Above- to belowground carbon allocation in peatlands shifts with plant functional type and temperature[#]

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Abstract

Background: Northern peatlands have accumulated vast amounts of carbon (C) as peat. Warming temperatures may affect peatland C stores by increasing microbial decomposition of ancient peat through enhanced input of labile root exudates by expansion of vascular plants, thereby accelerating atmospheric warming.

Aims: We set out to explore how much freshly assimilated C is allocated belowground by vascular plants, and if the above- to belowground allocation is affected by temperature and plant functional types.

Methods: We traced the C allocation pathways of two dominant plant functional types (i.e., sedges and shrubs) in two peatlands under different temperature regimes by combining selective plant removal in mixed sedge-shrub vegetation and in situ ^{13}C pulse-labelling. Aboveground to belowground C allocation as well as the C turnover were assessed by quantifying ^{13}C in plant leaves and soil respiration and by measuring $\delta^{13}C$ in dissolved organic C. A depth-resolved quantification of ^{13}C in the peat soil gave additional insight into belowground C allocation patterns.

Results: Temperature did not affect the rate at which ^{13}C was assimilated into shoots, but higher temperature decreased the fraction of assimilated C that was allocated belowground by vascular plants. Sedges assimilated CO_2 faster into their shoot biomass (faster depletion in ^{13}C in shoots) and allocated more of the assimilated ^{13}C belowground than shrubs. Conversely, sedges retained this belowground allocated C better than shrubs, leading to lower ^{13}C in soil respiration measured under sedges.

Conclusions: Climate induced vascular plant expansion will increase input of fresh assimilates into the peat substantially, even though part of this effect will be offset by reduced above- to belowground allocation rates. If shrub density increases relative to sedges, fresh assimilates are more likely to be respired than translocated to roots where they could reach and, potentially mobilize, ancient C stored in deeper peat layers.

KEYWORDS
^{13}C, climate change, peatland, pulse labelling, sedges, shrubs

1 | INTRODUCTION

Peatlands play an important role in the terrestrial carbon (C) cycle as they store one-third of the global soil C on only 3% of the land surface (Gorham, 1991; Turunen et al., 2002). The fate of this C store is uncertain, as high latitude temperatures are rising fast (IPCC, 2014), and decomposition might not be compensated through primary production as suggested for tundra ecosystems (Hartley et al., 2012). In addition, climate change can modify plant species dominance in peatlands by favouring the expansion of vascular plants at the expense of *Sphagnum* mosses (Bragazza et al., 2013). The shift from moss-dominated to vascular plant dominated conditions has strong implications for peatland C cycling.

Vascular plants have roots, grow faster and their litter is more easily decomposable than *Sphagnum* mosses (Dorrepaal et al., 2005; Limpens & Berendse, 2003). There is growing concern that climate-induced shift towards vascular plant dominated conditions will compromise the future C sink function of peatlands due to two main reasons: first, by reducing the rate of new peat formation as a result of increased decomposition rate of fresh litter (Zhang et al., 2019) and second by stimulating decomposition of existing peat. Reduced peat formation is attributed to the faster decomposition rate of vascular plant litter relative to *Sphagnum* litter due to the lower carbon-to-nitrogen ratio and differences in structural carbohydrates (Huang et al., 1998; Kaštovská et al., 2018; Schellekens et al., 2015). Enhanced decomposition of stored peat, including *Sphagnum*-derived remains, has been attributed to 'priming' as a result of root exudates (Basiliko et al., 2012; Walker et al., 2016). Low molecular weight organic compounds in the rhizosphere are expected to provide an easily degradable C source to microorganisms, thereby facilitating the breakdown of more recalcitrant older peat (Fontaine et al., 2007; Gavazov et al., 2018).

Clarifying how much of the freshly assimilated C is transferred belowground through roots, and if this above- to belowground allocation differs between plant growth strategies is crucial for understanding how peatland C storage will respond to changing temperatures. The majority of vascular plants in peatlands are divided into two plant functional types (PFTs): shrubs and sedges that represent contrasting growth strategies. This is particularly important, taking into account observed and predicted shifts in vegetation composition, that is, a greater increase of shrubs than of sedges (Heijmans et al., 2008; Jassey et al., 2013; Oke & Hager, 2020; Zeh et al., 2019). Sedges grow rapidly (Trinder et al., 2008) and assimilate CO_2 faster than their surrounding PFTs in peatlands (Ward et al., 2009). As their roots are equipped with aerenchym, they can root below the water table into older peat (Proctor & He, 2019), whereas shrubs are slowly growing and root shallower in the relatively younger peat (Murphy et al., 2009). Moreover, shrubs are suspected to have a greater root activity with warmer temperatures in comparison with sedges, that is, they provide a higher root C input to peatlands through higher root exudation rates and higher root turnover (Zeh et al., 2019). However, it is unclear how the differences in PFTs affect C input to peatlands. The belowground allocation of assimilated C and the effect on C turnover through root exudates are suspected to prime microbial decomposition of ancient peat (Gavazov et al., 2018; Walker et al., 2016), in particular at high temperatures. Ultimately, in a warming scenario, it is not known whether shrubs or sedges have a greater potential to activate the decomposition of old peat by this belowground labile C allocation.

To investigate how C dynamics is controlled by vegetation in peatlands, plant removal is a well-established method (e.g., Gavazov et al., 2018; Kuiper et al., 2014; Riutta et al., 2020; Ward et al., 2009). By removing the aboveground green biomass, photosynthesis and subsequent translocation of fresh C to the roots is disrupted. In a previous study, Zeh et al. (2019) utilized this short-term cessation of above- to belowground allocation to estimate the root C input by measuring soil respiration, dissolved organic carbon (DOC) and natural $\delta^{13}C$ in DOC. This mechanistic approach showed that sedges had a higher root-C input per gram plant biomass than shrubs. However, root-C input per area was lower because of low aboveground biomass of sedges, particularly at higher temperature. While giving a good approximation of total above- to belowground C allocation, this method gives limited mechanistic understanding of the C-allocation pathway.

Following up on the experiment design by Zeh et al. (2019), here we present the results of a selective clipping experiment with in situ ^{13}C pulse-labelling to quantify the recently assimilated C of two plant functional types (sedges and shrubs) at two peatlands with contrasting temperatures. In ^{13}C-pulse labelling experiments, C allocation patterns in plants can be investigated by temporarily enriching the atmosphere for photosynthesis with isotopically heavy $^{13}CO_2$ (i.e., adding a pulse of ^{13}C label) and tracing the heavy photosynthates as ^{13}C. We are particularly interested to assess the contribution of recently assimilated C to DOC and soil C respiration under field conditions. Furthermore, we examined the allocation of recently assimilated C at different peat depths during the field experiment. ^{13}C pulse-labelling allows to follow C through various parts of the plants into different soil fractions and its fate as CO_2 due to decomposition while only causing little disturbances to the ecosystem.

We hypothesized that the above- to belowground allocation of freshly assimilated ^{13}C is affected by plant functional type and site temperature. We expected that (1) sedges allocate more ^{13}C from above- to belowground than shrubs with the latter retaining relatively more ^{13}C in aboveground biomass and (2) a higher proportion of belowground translocated ^{13}C is respired at the high temperature site due to higher temperature-driven soil respiration.

2 | MATERIALS AND METHODS

2.1 | Study sites

Two *Sphagnum* dominated peatlands were selected in the Italian Alps along an altitudinal gradient so to represent a natural temperature gradient. The two peatlands, 'Lupicino' (1290 m asl) and 'Palù Tremole' (1700 m asl), differ in their mean annual temperature (MAT), which is 6.4°C (1981–2015) and 4.9°C (1992–2003 and 2013–2014), respectively (Zeh et al., 2019). Climate data were provided by the weather station in Deutschnofen for Lupicino, while temperature and precipitation

data for Palù Tremole were provided by the weather station in Fondo (987 m asl). Temperature data from Fondo were corrected for altitude by subtracting 0.6°C per 100 m increase in altitude. According to the differences in MAT, Lupicino is referred to as 'high temperature (T) site' and Palù Tremole as 'low temperature (T) site'. Annual precipitation was comparable between the low T site (825 mm, 1992–2003 and 2013–2014) and the high T site (810 mm, 1990–2015). During the first half of July 2016, water table levels at three piezometers on each site were lower in mean depth at the high T site (15.6 ± 2.7 cm; 27.9 ± 3.3 cm; 45.9 ± 3.3 cm) than at the low T site (11.0 ± 4.7 cm; 17.1 ± 3.6 cm; 28.0 ± 3.8 cm). The vegetation community on both sites is dominated by *Sphagnum magellanicum* (Brid.), *Sphagnum fuscum* (Schimp.), *Sphagnum capillifolium* (Ehrh.), *Calluna vulgaris* (L.) and *Eriophorum vaginatum* (L.). Further common species are *Vaccinium oxycoccos* (L.) and *Andromeda polifolia* (L.).

2.2 | Experimental design

On each of the two peatlands 20 hummocks co-dominated by shrubs and sedges were selected in June 2015. The plots were organized in five groups of four plots (experimental blocks) per peatland. Distance between plots within one block ranged between 1 and 20 m. Within each block, vegetation was selectively clipped to establish two plots with shrubs-only vegetation and two plots with sedges-only vegetation. One shrubs-only plot and one sedges-only plot were meant for control and remained unlabelled (no-label plots), whereas the other two plots (one shrubs-only plot and one sedges-only plot) were labelled with a ^{13}C pulse in July 2016 (label plots). The no-label plots were firstly clipped in June 2015, while the label-plots were firstly clipped in October 2015. Regrowth of the vegetation was removed in October 2015, May 2016 and July 2016.

The aboveground plant biomass on the label plots was smaller for sedges (low T: 34.4 ± 5.5 g m^{-2}; high T: 29.4 ± 6.9 g m^{-2}) than for shrubs (low T: 47.8 ± 5.5 g m^{-2}; high T: 74.7 ± 11.9 g m^{-2}). No significant difference in biomass was observed between sites ($p = 0.3$). Only for shrubs, the biomass was significantly higher on the high T site than on the low T site.

2.3 | In situ labelling experiment

Between the 9th and 30th July 2016, an in situ ^{13}C pulse-label was applied to the label-plots. To apply the ^{13}C pulse, each label-plot was covered with a transparent chamber (LDPE greenhouse film, 0.2 mm, UV5) of 85 dm^3 and 0.36 m^{-2} in size. The chamber frame was slightly pushed 1–2 cm into the moss surface. The edge between chamber and moss surface was covered with an overlap of 20 cm greenhouse film and weighted down with water bottles. The chamber was additionally fixed with taut cords to create a sealed atmosphere. The label was applied by dissolving 0.6 g of 99% ^{13}C-enriched sodium bicarbonate (Eurisotop, Cambridge Isotope Laboratories Inc., Tewksbury, USA) with 40 mL of sulfuric acid (5 M) which was injected through a septum embedded in the greenhouse film, resulting into an application of 238.3 mg ^{13}C per m^2. An axial flow fan (SEPA type MF_20C05L) ensured mixing of the air in the chamber and frozen thermal packs were used to reduce air temperature and condensation of water on the greenhouse film. All plots were labelled for 2 h and 12 min on sunny days between 10 AM and 2 PM. For eight plots, air temperature was logged within the chamber (iButton DS1922L, Maxim Integrated, San Jose, USA). During labelling, air temperature within the chambers increased to maximum 47°C and 50°C (low T and high T; Table 1), while air temperature outside the chambers was recorded between 25°C and 28°C (low T and high T; Table 1).

TABLE 1 Abiotic controls of labelling at two peatland sites [high and low temperature sites, high temperature (T) and low T, respectively]

	Low T site	High T site
Mean air temperature (°C) during label application	25	28
Air pressure (kPa) during label application	85	89
Maximum air temperature (°C) in labelling chamber	47	50
Calculated $\delta^{13}C$ in label chamber	72608	71906

2.4 | Estimation of $^{13}CO_2$ back-diffusion and ^{13}C assimilation by mosses

To estimate the influence of ^{13}C diffusion into the peat on soil respiration, DOC and peat, two additional plots were established on the low T site. These plots were selected in the same way as stated above, but all vascular plants were removed in July 2016 (hereafter named 'moss plots'). The two plots were labelled in the exactly same manner, but one moss plot was completely covered by an opaque labelling chamber (opaque chamber), while the other moss plot was labelled with a regular transparent labelling chamber (transparent chamber). Both plots were equipped with exactly the same set-up of pore water sampling and soil respiration rings as all the other plots and peat cores were taken at the same point in time. The opaque chamber enabled us to assess potential importance of diffusion of label into the peat. As photosynthesis is inhibited by the opaque cover, any enrichments in soil respiration, DOC and peat subsamples are assumed to be a result of diffusion processes. The transparent chamber enabled us to estimate at which time after labelling the influence of vascular plants on soil respiration is bigger than ^{13}C back-diffusion and moss together by comparing the enrichment in soil respiration of all treatment plots with the labelled moss plot. In addition, the peat subsamples of the labelled moss plot (transparent chamber) also allowed us to estimate the depth wherein mosses assimilate and translocate C.

2.5 | Shoot sampling

Directly after label application, a small amount of sedge and shrub shoots was sampled from each label and no-label plot. Seven days after labelling, the aboveground PFT's biomass on all label-plots was collected, meaning all biomass above the moss layer including woody tissues. The biomass samples were freeze-dried and weighed. Then, all samples were milled with a Fritsch mill pulverisette 23, and $\delta^{13}C$ was analyzed using an Elementar PYRO cube coupled to the visION IRMS (Isoprime, Elementar Analysensysteme GmbH, Langenselbold, Germany).

2.6 | Soil respiration measurement and calculation

For soil respiration measurements, two PVC collars (KG DN110, inner diameter of 10.4 cm, 8 cm height) were inserted 5–7 cm into the peat soil in each plot. The collar installation took place in May 2016 to avoid installation effects on soil respiration measurements during the in situ ^{13}C pulse-labelling experiment in July 2016. Inside the collars, all green leaves of vascular plants and mosses were removed to avoid plant respiration during soil respiration measurements. To prevent drying of the peat inside the collars, a thin fleece was placed on the bare peat surface in the collars in between soil respiration measurements (Zeh et al., 2019).

Soil respiration was measured in a closed dynamic system with an opaque chamber fitting on the PVC collars. The chamber was connected to the Cavity Ring-down Spectroscopy device (CRDS; Picarro G2201-I, Picarro Inc., Santa Clara, USA). Two sets of chambers with corresponding tubes were available of which one set was exclusively used to measure soil respiration in no-label plots to avoid any label contamination. Between soil respiration measurements, the tubes were flushed with atmospheric air to prevent carry-over effects of the label between treatments.

Soil respiration measurements were conducted on each plot directly after labelling and 6–14 times more in regular time steps within 7 days after labelling (excluding the plots used for estimation of $^{13}CO_2$ back-diffusion). For all measurements, $\delta^{13}C$ of plant induced soil respiration was calculated as described in the upcoming section to calculate the amount of respired ^{13}C from the labelling.

Soil respiration was defined as positive CO_2 flux from the soil to the atmosphere. In each soil respiration measurement by the CRDS device, $\delta^{13}C$ in CO_2 was recorded every few seconds and thus $^{13}CO_2$ and $^{12}CO_2$ concentrations were deduced. Of each measurement, which on average lasted for 7 min 20 s, the first and last 10% of the data were excluded to minimize chamber docking effects. To calculate the total soil respiration, single linear models were fitted to the sum of $^{13}CO_2$ and $^{12}CO_2$ increase in the headspace of the chamber. Mean R^2 of all 497 fitted soil respiration measurements was 0.99 ± 0. Soil respiration R_S (μmol C m^{-2} s^{-1}) was calculated according to Equation (1) based on the volumetric concentration change over the sampling time dc/dt (ppm s^{-1}), the chamber volume V (m^{-3}), the covered area A by chamber (m^{-2}), the air pressure p, the gas constant R (m^3 Pa K^{-1} mol^{-1}), the chamber temperature T (K), the molar mass M (g mol^{-1}) and the proportion of C in CO_2 Z:

$$R_S = \frac{dc}{dt} \times \frac{M \times p \times V \times Z}{R \times T \times A} \quad (1)$$

2.7 | $\delta^{13}C$ of plant induced soil respiration and respired ^{13}C by label plots

To separate sources of soil respiration, a two-pool isotope mixing model (Equation 2) was applied, which finds its application in many ^{13}C pulse-labelling experiments (e.g., Biasi et al., 2012). The initial ambient air CO_2-concentration m_1 and the corresponding $\delta^{13}C$ in air F_1 are mixed with CO_2 from soil respiration m_2 with a specific $\delta^{13}C$ F_2 and add up to the CO_2-concentration m_Σ with $\delta^{13}C$ F_Σ. Note that 398 ppm (m_1) and 490 ppm (m_Σ) CO_2 concentration in the chamber headspace were set as target concentrations to feed the two-source mixing model.

$$F_2 = \frac{m_\Sigma \times F_\Sigma - m_1 \times F_1}{m_\Sigma - m_1} \quad (2)$$

The corresponding $\delta^{13}C$ to the target concentrations (F_1, F_Σ) in each soil respiration measurement was calculated by linear models fitted to $\delta^{13}C$ increase or decrease (label or no-label treatment). Note that 398 ppm was chosen because it equals ambient $^{12}CO_2$ concentration in the air. $^{12}CO_2$ concentration of 490 ppm in the chamber headspace occurred within a linear increase of CO_2 soil respiration and was covered in more than 75% of all soil respiration measurements. Forty-six measurements were excluded because their actual measurement range did not overlap to 75% with the target concentration range.

The amount of respired $^{13}C_R$ (μg m^{-2} s^{-1}) originating from labelling was calculated by using another two-source mixing model (Equation 3). The equation considers R_S (Equation 1), the initial $\delta^{13}C$ in the labelling chamber $F_{chamber}$ (Table 1), F_{label} and $F_{no\text{-}label}$ (both from Equation 2). But for $F_{no\text{-}label}$, one mean value for the experiment was deduced per PFT and site (Table 1).

$$^{13}C_R = \left(1 - \frac{F_{label} - F_{chamber}}{F_{no-label} - F_{chamber}}\right) \times R_S \quad (3)$$

To describe $\delta^{13}C$ dynamics in the soil respiration from the label plots per PFT and site and to estimate the total respired ^{13}C over time, exponential decay functions (Equation 4) were fitted to the $\delta^{13}C$ and respired $^{13}C_R$ data. In case of respired $^{13}C_R$, the decay function was integrated over the experiment time of 7 days. We did not consider the measurements of the first 24 h for integration calculation because they were dominated by back-diffusion processes and not respiration (see Section 3.3.2; Gavrichkova et al., 2018; Subke et al., 2009).

$$^{13}C_R = e^{\alpha}_{Site,\ PFT} + \beta_{Site,\ PFT} \times time + \gamma_{Site,\ Block} + \varepsilon \quad (4)$$

To estimate the back-diffusion effect on soil respiration, ^{13}C in soil respiration on the label-moss plots and soil respirations in the first 24 h after label application of treatment plots were expressed as atom% excess. $^{13}C/^{12}C$ ratio ^{13}R in soil respiration was determined by

transforming the fixed reference values F_2 (Equation 2) into its proportion.

$$Atom\,\%\,excess = \left(\left[\frac{^{13}R}{(^{13}R+1)} \right]_{label} - \left[\frac{^{13}R}{(^{13}R+1)} \right]_{no-label} \right) \times 100 \quad (5)$$

Total recovery of ^{13}C over 7 days was calculated by the ^{13}C recovery in biomass after 7 days and the accumulated sum of respired $^{13}C_R$ over 7 days.

$$^{13}C_{recovery} = {}^{13}C_{biomass\ day\ 7} + \int_{day\ 0}^{day\ 7} e^{\alpha_{site,\ plot} + \beta_{site,\ plot} \times time} \quad (6)$$

2.8 | Peat core sampling

In addition to the soil respiration measurements, peat cores were extracted on the second day after labelling from each label plot. The second day after labelling was selected because we assumed that ^{13}C allocation into the soil would be highest (Subke et al., 2012), while ^{13}C decomposition would still be minor (Zeh et al., 2019). The peat cores that served as no-label reference were taken the day before labelling right on the edge of the label plots. The sampling was conducted with a custom-made metal peat corer and a knife to avoid that the peat cores were compacted. During field campaign in July 2016, the peat cores were first cooled to 8°C and later frozen to −20°C. From each set of the collected peat cores (2 sites × 2 PFTs × 5 experimental blocks = 20 cores in total), one was selected for each site and PFT (low T sedge, low T shrub, high T sedge and high T shrub) based on the smallest deviation from the mean weight of the respective PFT on each site. The aim was to assess the appropriate depth increments to characterize vertical changes in ^{13}C distribution as a result of root-inputs, by comparing cores from label and no-label plots. The four selected peat cores were cut into 10 increments of 2 cm depth after being frozen. To eliminate any potential ^{13}C contamination from the top to bottom during peat core sampling, we thinly scraped and discarded outer core material. All subsamples were freeze-dried, milled and measured as described in Section 2.5. The preliminary results of ^{13}C distribution with depth revealed an optimal increment pattern of 0–5 cm, 5–8 cm, 8–12 cm, 12–16 cm, and 16–20 cm, which was applied to the remaining label peat cores. The increments were freeze-dried and then assorted into two subsamples: 200–250 mg of pure moss-derived peat and residual bulk peat (composed of vascular plant tissue and surrounding moss-derived peat).

Four peat cores were chosen to serve as no-label reference by the smallest deviation from the mean weight of the respective PFT on each site. They were processed in the same way as the remaining label peat cores, that is, cut into the five increments (0–5 cm; 5–8 cm; 8–12 cm; 12–16 cm; 16–20 cm) and divided into two subsamples.

2.9 | Dissolved organic carbon

To collect pore water, two mini-rhizons (Rhizosphere, 10 Rhizon SMS 10 cm) per plot were inserted into 5–15 cm soil depth 1 day before labelling. The syringes were connected to the mini-rhizons and protected against ultraviolet (UV) light by aluminium foil. The first sample was discarded due to potential installation effects. Immediately after label application, the syringes were put on vacuum, and pore water was collected the following morning (day 1 sampling). The next pore-water samples were collected in the morning of days 3 and 8 of the experiment, applying the vacuum at the previous afternoon. Day 1 sampling should reflect the cumulative effect during the first 15–20 h, while days 3 and 8 samplings were intended to reflect the potential later allocation of assimilates from above- to belowground pools. The sampling times were a compromise between temporal resolution and practical constraints of obtaining pore water. DOC samplings were simultaneously done for the corresponding no-label plots. During the field campaign, all DOC samples were cooled to 8°C and then stored at −20°C until measurement.

Pore water samples were pre-acidified with ± 20 µL of 37% HCl to pH 2, and DOC concentration (mg L^{-1}) was analyzed with a TOC analyzer (Elementar vario TOC cube). Combustion temperature was 850°C, and quantification was done with a non-dispersive infrared detection system. ^{13}C stable isotope analysis was carried out using a combined system of high-temperature combustion (HTC)-based TOC analysis and Isotope Ratio Mass Spectrometry developed by Federherr et al. (2014). Injection volume for the pre-acidified samples was 0.5 mL. Combustion by oxygen took place at 850°C and the $\delta^{13}C$ ratio (‰) was analyzed relative to the Vienna Pee Dee Belemnite standard using an isotope ratio mass spectrometer (isoprime visION). Further details of this analysis are provided by Leinemann et al. (2018), and all calculations for corrections and normalization were done according to those described in Kirkels et al. (2014).

2.10 | Statistical analyses

Mean values in all figures and written results section are presented with standard errors. Data handling, statistics and figures were accomplished with R 3.6.3 (R Core Development Team, 2020). Hypothesis tests were conducted with Wilcoxon Signed Rank Test as the numbers of replicates differed between groups or requirements for parametric tests were not met. An overview of all samples with the number of replicates is listed in Table S1. Explanatory variables for log 10 transformed respired ^{13}C over 7 days were estimated by a linear mixed model with the *lme()* function of the *nlme4* package in R (Pinheiro et al., 2019). The applied model accounts for the fixed effects of the sites and PFTs over time and their interaction, and the random effect of the five experimental blocks for each site separately. Model estimates of explanatory variables are reported in Table S6a and S6b. Figures illustrating the decrease in $\delta^{13}C$ in soil respiration and decrease in respired ^{13}C (Figures 1 and S5, respectively) are based on the linear mixed model estimates. The cumulative estimation of respired ^{13}C from soil over 7 days for each treatment combination was conducted by log 10 transformation of respired ^{13}C data, linear regression with *lm()* function (Table S6c) and subsequent application of the *integrate()* function.

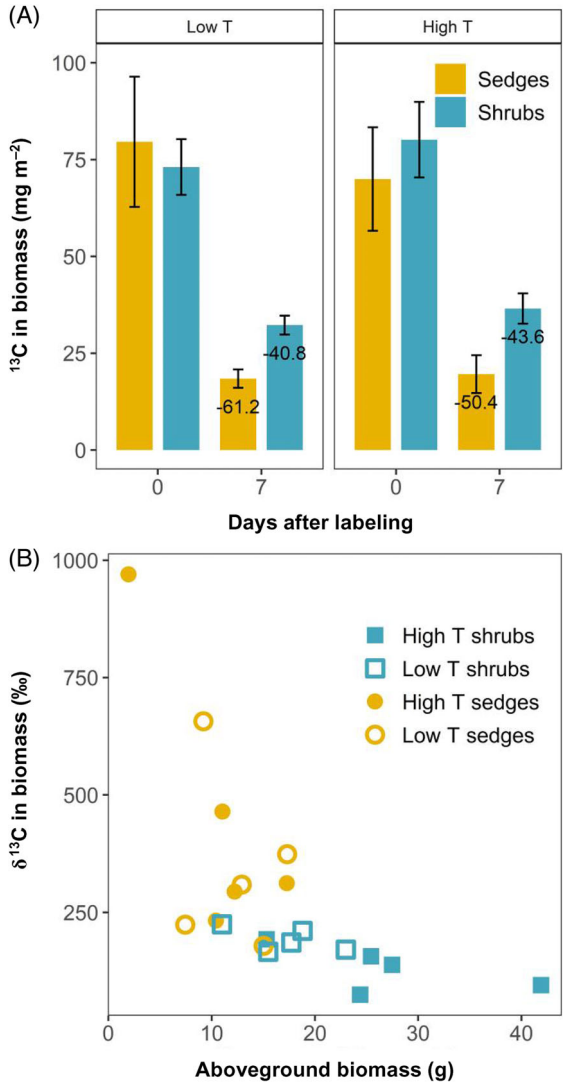

FIGURE 1 (A) Retained amounts of ^{13}C in aboveground biomass of shrubs (*C. vulgaris*) and sedges (*E. vaginatum*) at two peatland sites (high and low temperature sites, high temperature (T) and low T, respectively) directly (day 0) and 7 days after labelling. Numbers in the figure represents the relative loss of ^{13}C in the aboveground biomass from 0 to 7 days after labelling. (B) Inverse relationship between the enrichment in δ^{13}C of shoot biomass of shrubs and sedges directly after labelling (day 0) and shoot biomass per plot at two peatland sites differing in temperature (high and low temperature sites, high T and low T, respectively)

3 | RESULTS

3.1 | δ^{13}C and ^{13}C in plant biomass

Immediately after labelling, the δ^{13}C in aboveground biomass was higher in sedges than shrubs, particularly at the high T site. Here, sedges assimilated significantly more ^{13}C per gram biomass than shrubs (Table 2). When expressed relative to the surface area, the ^{13}C in the aboveground biomass was similar between PFTs and sites, that is 75.7 ± 5.7 mg ^{13}C m^{-2} (Figure 2A; $p = 0.9$), because of an inverse relationship between vascular plant biomass and δ^{13}C, with higher enrichment in plots with lower vascular plant biomass, that is, in plots with sedges (Figure 2B). Seven days after labelling, the ^{13}C in the aboveground biomass decreased strongly compared to the beginning of the experiment and was significantly lower in sedges than in shrubs (Figure 2A).

TABLE 2 Amount of ^{13}C per g dry weight (dw) aboveground biomass of shrub (*C. vulgaris*) and sedge (*E. vaginatum*) at two peatland sites (high and low temperature sites, high temperature (T) and low T, respectively) directly after labelling (day 0)

	^{13}C in above-ground biomass (mg ^{13}C × g dw^{-1}) on day 0
Low T sedges	2.4 ± 0.5
Low T shrubs	1.6 ± 0.1
High T sedges	3.0 ± 0.8
High T shrubs	1.1 ± 0.2

3.2 | Dissolved organic carbon and DO^{13}C

DOC concentrations in all plots (label- and no-label plots) were significantly higher at the high T site with 48.4 ± 2.0 mg L^{-1} compared to the low T site with 28.6 ± 0.7 mg L^{-1} (Figure S2). ^{13}C recovery in DOC over the period of 7 days was very low, and δ^{13}C in DOC showed no distinct changes after labelling (Figure S3). At the high T site, the highest enrichment in δ^{13}C did not exceed 0.5‰ (sedges on day 3) compared to the no-label plots. At the low T site, label plots were even depleted in δ^{13}C [−0.6–(−0.1) ‰] compared to the no-label plots. In addition, no ^{13}C enrichment was found in plots where diffusion effects were tested, suggesting that temporarily high δ^{13}C in porous air did not affect δ^{13}C in DOC (Figure S4).

3.3 | Soil respiration, total respired ^{13}C and δ^{13}C dynamics in respired CO_2

3.3.1 | Treatment effects

The amount of ^{13}C recovered from aboveground biomass and soil respiration after 7 days (from the applied 238.3 mg^{13}C m^{-2}) was lower for sedges than for shrubs (Table 3). Also, the amount ^{13}C respired from the soil over 7 days calculated by exponential decay function (Figure S5; Table S6c) was lower for sedge plots than for shrub plots (Table 3). The difference in respired ^{13}C between PFTs (10 mg ^{13}C m^{-2} at both sites) was bigger than the difference between sites (6.5 mg ^{13}C m^{-2} for both PFTs), implying that the PFT effect was stronger than the T effect. Throughout the observation time, the lowest δ^{13}C in soil respiration was observed under sedges at the high T site (Figure 1, Table S6b).

Mean soil respiration was significantly higher at the high T site compared to the low T site for both label and no-label plots

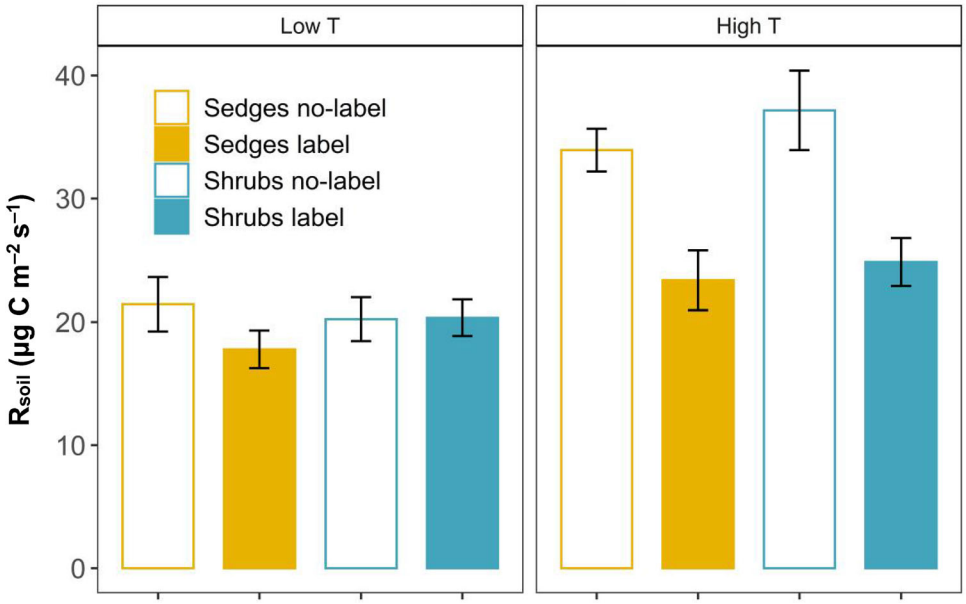

FIGURE 2 Mean soil respiration rates over 7 days after labelling for the label and no-label plots of shrubs (*C. vulgaris*) and sedges (*E. vaginatum*) at two peatland sites [high and low temperature sites, high temperature (T) and low T, respectively]

TABLE 3 Respired ^{13}C, sum of respired ^{13}C and ^{13}C in aboveground biomass, and total recovered ^{13}C

	Respired ^{13}C (mg ^{13}C m^{-2}) from soil over 7 days	Respired ^{13}C + ^{13}C in aboveground biomass on day 7 (mg ^{13}C m^{-2})	Recovery of ^{13}C after 7 days relative to applied ^{13}C (%)
Low T sedges	18.7	37.1	16
Low T shrubs	28.8	61.1	26
High T sedges	12.4	31.8	13
High T shrubs	22.3	58.8	25

(Figure 3). No-label plots showed significantly higher mean soil respiration rates than the label-plots suggesting that root decomposition was more advanced due to 4 months earlier first plant removal (Figure 3).

3.3.2 | Influence of back-diffusion

Directly after labelling, ^{13}C enrichment in soil respiration from the label-moss plots (no vascular plants were present) was five to seven times higher than in the other label plots (Table S7), indicating a strong impact of diffusive flow of label into the porous moss layer. This enrichment in the label-moss plots, that is, the plots with the highest diffusion gradient into the soil, decreased to a level similar or even lower than all the other plots within 24 h after labelling however, indicating that the impact of diffusion was transient and unlikely to influence label recovery in DOC, soil respiration and peat. By considering soil respiration data measured only later than 24 h after labelling (Gavrichkova et al., 2018; Subke et al., 2009), we made sure that the observed patterns are due to the treatment effects and not back-diffusion (see Section '2.6 Soil respiration measurement and calculation').

3.4 | Peat

3.4.1 | Treatment effects

We observed a significantly higher ^{13}C enrichment in the bulk peat compared to the pure moss-peat subsample under both PFTs and on both studied sites after 2 days ($p < 0.001$; Figure 4A), confirming that ^{13}C was transmitted into the peat through vascular tissues. The ^{13}C enrichment in the peat was highest under sedges at the low T site (Table 4). Overall, in the peat from the high T site, a lower enrichment was observed (Table 4, Figure 4A). ^{13}C enrichment decreased significantly with depth (sum of subsamples per increment), irrespective of PFT ($p < 0.05$) and site (Figure 4A).

Mean recovery of ^{13}C in the bulk peat, as expressed per gram of PFT aboveground biomass, varied considerably, but a higher enrichment was found under sedges compared to shrubs for all depth increments

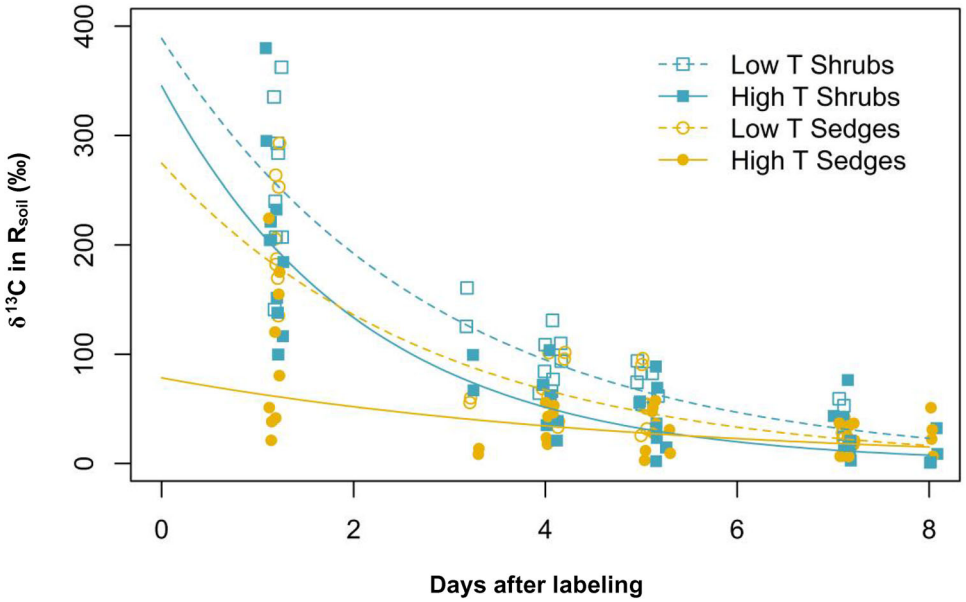

FIGURE 3 Decrease of $\delta^{13}C$ in soil respiration described by exponential decay function for shrubs (*C. vulgaris*) and sedges (*E. vaginatum*) at two peatland sites differing in temperature (high and low temperature sites, high T and low T, respectively). Decay functions were fitted to data past 24 h after labelling

TABLE 4 Sum of ^{13}C in peat cores sampled on the second day after labelling at two peatland sites (high and low temperature sites, high T and low T, respectively) under shrubs and sedges. Numbers give the sums of all subsamples and all depth increments as means with standard error (SE)

	Sum of ^{13}C over all increments (mg)
Low T sedges	0.35 ± 0.10
Low T shrubs	0.24 ± 0.04
High T sedges	0.15 ± 0.02
High T shrubs	0.14 ± 0.02

(Figure 4B). Moreover, under sedges more ^{13}C was recovered deeper in the peat than under shrubs, irrespective of temperature. Under shrubs, the enrichment in ^{13}C was clearly highest in the top 5 cm and tended to be lower at the high T site than at the low T site (Figure 4B).

3.4.2 | Influence of mosses and back-diffusion

In the label-plot without vascular plants (moss plots) and with the transparent chamber, only the top 2 cm of the peat core was enriched in ^{13}C, suggesting limited contribution of mosses to belowground C allocation (Figure S8). In the opaque chamber, a small enrichment occurred in the top 2 cm (Figure S8), suggesting that during labelling, the $^{13}CO_2$ gradient between the chamber and the soil pores stayed at a high level throughout the labelling time. The $^{13}CO_2$ gradient and thus the amount of diffused $^{13}CO_2$ were possibly higher compared to all other plots. The enrichment in the top 2 cm probably occurred after labelling within the first 24 h when $^{13}CO_2$ diffused back into the atmosphere. But since this effect was marginal, we considered the peat cores to be not influenced by back-diffusion of $^{13}CO_2$.

4 | DISCUSSION

4.1 | ^{13}C in aboveground biomass—Faster assimilation by sedges irrespective of temperature

The assimilated ^{13}C per gram of biomass was significantly higher for sedges than for shrubs (Table 2). It is known that sedges not only assimilate more C, but also faster than shrubs (Ward et al., 2009). Hence, the disproportional enrichment in ^{13}C per unit sedge biomass is a further proof for their high C assimilation, confirming our first hypothesis. However, sedges also appeared to have a faster C turnover in their aboveground biomass considering the greater depletion of ^{13}C in the shoot biomass relative to shrubs 7 days after the labelling (Figure 2A: low T: −61.2 mg m^{-2} and high T: −50.4 mg m^{-2}; likewise found in Ward et al., 2009). Carbon assimilation rates were not affected by temperature.

4.2 | ^{13}C in peat—More C allocated belowground under sedges than shrubs

The highest enrichment of ^{13}C in the peat was found in the top 5 cm where both the photosynthetically active layer of *Sphagnum* and overgrown vascular green plant tissues are still located (Figure 4A). *Sphagnum* is known to efficiently assimilate CO_2 (Woodin et al., 2009) and

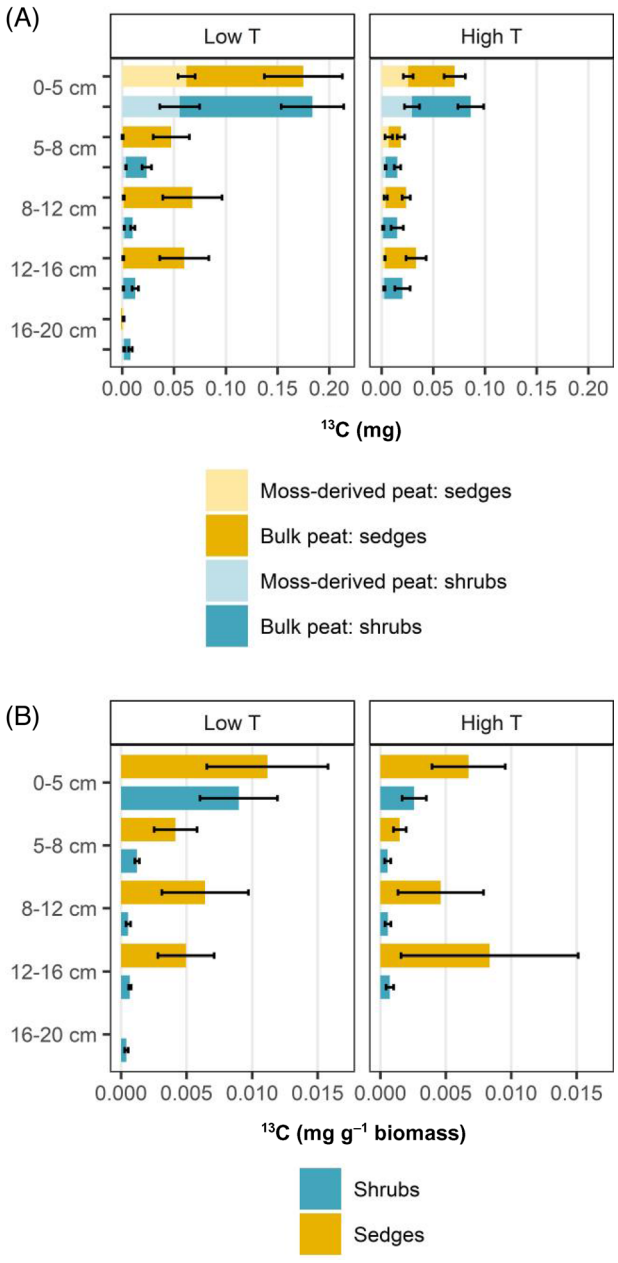

FIGURE 4 (A) Belowground allocated ^{13}C in peat cores sampled on the second day after labelling at two peatland sites (high and low temperature sites, high temperature (T) and low T, respectively) under shrubs and sedges. Stacked bars represent means with standard error (SE) per increment of moss-derived peat subsample and bulk peat subsample under the respective vascular plant. Moss-derived peat represents pure residues of moss (withouth any visible vascular plant constituents), whereas bulk peat represents both residues of vascular plant tissues and moss-derived peat. (B) Belowground allocated ^{13}C per gram aboveground biomass in peat cores sampled on the second day after labelling at two peatland sites (high and low temperature sites, high T and low T, respectively) under shrubs and sedges. Bars represent means of ^{13}C in the bulk peat subsamples divided by the amount of aboveground biomass

to keep the majority of assimilates in the top 5–8 cm (Fenner et al., 2004). However, in our study, the higher ^{13}C enrichment in the bulk peat subsamples (including vascular plant tissues) compared to the pure moss-derived peat (Figure 4A) suggests that vascular plants were also responsible for the enrichment in the uppermost 5 cm of the peat.

Less freshly assimilated C was recovered in the peat at the high T site than at the low T site, even when aboveground biomass (for shrubs) was highest at the high T site (Figure 4A). Apparently, temperature-induced increases in aboveground biomass do not necessarily translate into fresher photosynthates allocated belowground. This discrepancy can be potentially explained by temperature that (1) reduces the efficiency in above- to belowground C translocation and/or (2) reduces the root:shoot biomass ratio. If the first explanation was applied, one would expect a reduction in ^{13}C recovered in the peat under sedges at the high T site as the aboveground sedge biomass did not differ between sites. Indeed, this is true for sedges (Figure 4A). Additionally, one would expect a reduction in ^{13}C recovered in peat per sedge biomass. Instead, we found a rather equal ^{13}C recovered per sedge biomass (Figure 4B). Consequently, shifts in root:shoot biomass ratio seem to be the more likely explanation for sedges. Shifts in root:shoot ratio in response to warming have been reported from warming experiments in arctic fens (Sullivan et al., 2008), tundra ecosystems (Hobbie & Chapin III, 1998; Tian et al., 2020; Wang, Mommer et al., 2016) and mineral soils (Dietzen et al., 2019). For shrubs, a reduced efficiency in belowground C translocation is a more plausible explanation because ^{13}C recovered per shrub biomass decreases with warming (Figure 4B) and because an increase in root:shoot biomass with warming is reported in particular for *Calluna* species (Hobbie & Chapin III, 1998; Malhotra et al., 2020). Additionally, Gavrichkova et al. (2018) recovered small ^{13}C amounts belowground in a labelling experiment on Mediterranean shrubs and hypothesized that ericaceous shrubs tend to feed their root growth rather on reserves than on freshly assimilated C, implying that a higher belowground allocation by shrubs could still occur later than 2 days after the label application.

Although we observed a significant decrease in ^{13}C from the top 5 cm to deeper increments under both PFTs (Figure 4A), the translocated ^{13}C per gram of aboveground biomass was not decreasing with peat depth under sedges. Up to a depth of at least 16 cm, sedges allocate more freshly assimilated C per unit of biomass into the peat soil than shrubs (Figure 4B), confirming our first hypothesis. This seems a combined effect of higher C allocation efficiency of sedges compared to shrubs together with a higher sedge root presence. In a tundra ecosystem, 89% of the total sedge biomass was found belowground (Woodin et al., 2009). Additionally, sedges in contrast to shrubs show a strong belowground response to growing seasons, when they form roots every year anew (Wang, Mommer et al., 2016).

In contrast to sedges, a stronger decreasing trend with depth in allocated ^{13}C per unit biomass was observed under shrubs (Figure 4B), reflecting the difference in depth distribution of rooting systems. Shrubs tend to have a shallower rooting system, while sedges can have roots which reach deep into the peat (Murphy et al., 2009). Indeed, shrubs potentially invested more of the added ^{13}C label into shallow

belowground plant tissues, for example, branches, than into deep roots (align with Murphy & Moore, 2010; Figure 4A).

4.3 | Lower ^{13}C soil respiration under sedges than under shrubs at higher temperature

The amount of assimilated ^{13}C per unit of the surface area indicates a homogeneous uptake of label across PFTs, irrespective of temperature (Figure 2A). However, less ^{13}C was respired under sedges than under shrubs (Table 3; −20 mg m^{-2}) and more was retained belowground in the peat. These results imply that sedges have a loose and slower coupling between photosynthesis, C allocation into the soil and subsequent soil respiration compared to shrubs. Equally important, the amount of respired ^{13}C during 7 days was lower at the high T site than at the low T site for both PFTs (Table 3), a result contradicting our second hypothesis. As we found evidence of lower root biomass under sedges and lower efficiency in belowground translocation under shrubs at the high T site, both processes could have reduced ^{13}C soil respiration due to lower autotrophic respiration.

4.4 | Limitations of selective clipping and ^{13}C labelling in the field

Although the majority of vascular plant biomass in peatlands is belowground (Wang, Heijmans, et al., 2016) and surface DOC has been reported to be highly influenced by vegetation (Tfaily et al., 2018), we found no ^{13}C in DOC. In a laboratory labelling approach, Fenner et al. (2007) found that assimilated ^{13}C in DOC accounted for 0.5% at its peak 5 h after the pulse. Therefore, under field conditions, it could mean that either only small amounts of root-derived C were exuded by vascular plant roots or this C was directly mineralized by microbes. However, we conclude that DOC is a minor C pool for root C allocation by vascular plants.

Not only in DOC, but also the overall recovery of ^{13}C was relatively low. On the one hand, we did not fully consider belowground allocation by roots but rather kept the plots intact for soil respiration and pore water samplings. On the other hand, the recovery term for in situ labelling in peatlands is likely anyway low due to (1) the open system and (2) generally slow assimilation rates of the vegetation.

4.5 | Further implications for C-cycling in peatlands under future warmer conditions

In this study, we firstly measured the lowest $\delta^{13}C$-ratios in soil respiration under sedges at high T and secondly significantly higher soil respiration rates at the high T site. Both results together imply that comparatively more C from non-labelled sources was respired under sedges at high T, which can be interpreted as higher decomposition under sedges than under shrubs at higher temperatures. In a previous study, we found indeed indications of an increased decomposition of moss-derived peat under sedges (Zeh et al., 2020). This long-term pattern is possibly reflected in the corresponding short term C dynamic. The high translocation of readily available C by sedges coincides with a high temperature sensitivity of the rather old peat for decomposition (Hilasvuori et al., 2013). Both together results in the observed stronger peat decomposition under sedges at elevated temperatures (Zeh et al., 2020). Apart from that, sedge roots are known to trigger decomposition by providing oxygen through their aerenchym (Armstrong, 1964; Holzapfel-Pschorn et al., 1986; Roura-Carol & Freeman, 1999). Additionally, fresh sedge roots themselves were shown to be highly decomposable (Wang et al., 2017) and, as a consequence of their deep rooting depth sedge roots may affect relatively older peat than shallow rooting PFTs. Hence, sedge root biomass might play a key role for both short- and long-term peat decomposition dynamics in peatlands.

5 | CONCLUSION

Our results indicate that above- to belowground C allocation in peatlands differs between sedges and shrubs and that this C allocation is dependent on temperature. Sedges have a greater aboveground C assimilation rate than shrubs. From the above- to belowground translocated C, under sedges more C is retained belowground, while under shrubs more freshly assimilated C is respired. Additionally, our results show that less of the newly assimilated C was respired with higher temperatures, most likely because vascular plants interact with temperature and invest relatively less into belowground biomass, that is, roots, and potentially more in aboveground biomass at elevated temperature. When extrapolating this result, it could mean that under climate change, root-driven C-cycling in peatlands might become less important compared to the direct effects associated, for example, to an increase of peat aeration.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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