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Vascular plant-mediated controls on atmospheric carbon assimilation and peat carbon decomposition under climate change

Running head: Vascular plants and peat carbon cycling

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Abstract

Climate change can alter peatland plant community composition by promoting the growth of vascular plants. How such vegetation change affects peatland carbon dynamics remains, however, unclear. In order to assess the effect of vegetation change on carbon uptake and release, we performed a vascular-plant removal experiment in two *Sphagnum*-dominated peatlands that represent contrasting stages of natural vegetation succession along a climatic gradient. Periodic measurements of net ecosystem CO_2 exchange revealed that vascular plants play a crucial role in assuring the potential for net carbon uptake, particularly with a warmer climate. The presence of vascular plants, however, also increased ecosystem respiration, and by using the seasonal variation of respired CO_2 radiocarbon (bomb-^{14}C) signature we demonstrate an enhanced heterotrophic decomposition of peat carbon due to rhizosphere priming. The observed rhizosphere priming of peat carbon decomposition was matched by more advanced humification of dissolved organic matter, which remained apparent beyond the plant growing season. Our results underline the relevance of rhizosphere priming in peatlands, especially when assessing the future carbon sink function of peatlands undergoing a shift in vegetation community composition in association with climate change.

INTRODUCTION

Peatlands are formed under climatic, hydrological and biological conditions that suppress the decomposition of plant litter, resulting in the accumulation of organic matter as peat. The imbalance between litter production and decomposition makes peatlands effective long-term sinks of atmospheric carbon (Yu, 2012). Indeed, despite a distribution limited to c. 3% of the Earth's land surface, peatlands contain c. 30% of its soil carbon (Yu, 2012). In northern peatlands, *Sphagnum* mosses play a crucial role in peat accumulation due to the production of litter particularly resistant to microbial decomposition (Hájek *et al.*, 2011). However, alteration of the hydrological balance (Talbot *et al.*, 2014; Munir *et al.*, 2015), increase in nitrogen availability (Bubier *et al.*, 2007; Juutinen *et al.*, 2010) and, more specifically, climate warming (Weltzin *et al.*, 2000; Dieleman *et al.*, 2015) can promote the growth and cover of vascular plants in peatlands. Such increase in the abundance of vascular plants can potentially reduce the productivity of *Sphagnum* mosses due to, for example, lower light availability (Chong *et al.*, 2012) and increasing evapotranspiration (Hirano *et al.*, 2016). In addition, considering that the decomposition rate of vascular plant litter is much faster than that of *Sphagnum* mosses (Dorrepaal, 2007), it is crucial to clarify the role of a higher vascular plant biomass, particularly with a warmer climate, with reference to the capability of the system to act as carbon sink (Breeuwer *et al.*, 2010; Ward *et al.*, 2013; Wang *et al.*, 2015).

From a belowground biogeochemical perspective, the presence of vascular plants can supply soil microbes with labile carbon substrates via rhizosphere exudates, providing additional energy to invest in decomposition of old organic matter (Fontaine *et al.*, 2007; Schmidt *et al.*, 2011): a process known as the priming effect (Kuzyakov, 2010). Nevertheless, it is still unknown whether the priming effect in peatlands is directly linked to the abundance of vascular plants, and whether

the priming effect shows any seasonal trend, particularly in relation to plant phenology. Answering these questions can help to better predict how climate warming will alter the carbon cycle of northern latitude peatlands when vascular plants become more abundant (Dieleman *et al.*, 2015) and the length of the growing season increases (Piao *et al.*, 2008).

To investigate the role of vascular plants in the seasonal net assimilation of atmospheric carbon and in the decomposition of peat carbon under contrasting climatic conditions, we performed a vascular plant-removal experiment in two *Sphagnum*-dominated peatlands that were located at different elevations and thereby naturally differed in mean annual temperature, growing season length and vascular plant abundance (Table 1). As such, the comparison of our study sites should be interpreted as a space-for-time substitution (Blois *et al.*, 2013), whereby the low elevation peatland represents the ecosystem state resulting from a natural response of vegetation to warmer climate compared to the upslope site (Klaus, 2007). During a full growing season, we periodically measured the net ecosystem CO_2 exchange (NEE), the ecosystem respiration (R_{eco}) and its radiocarbon signature, and the humification degree of dissolved organic matter in order to: 1) assess the role of vascular plants in assimilation of atmospheric CO_2 compared to *Sphagnum* mosses under contrasting climatic conditions; and 2) detect any temporal link between the presence of vascular plants and enhanced decomposition of peat through rhizosphere priming and the associated carbon release into both the atmosphere and pore water.

MATERIAL AND METHODS

Study sites and experimental design

We selected two *Sphagnum*-dominated peatlands located at 1035 m and 1885 m a.s.l. in Switzerland (Table 1, Table S1). At both sites, dominant vascular plant species were *Eriophorum*

vaginatum, *Calluna vulgaris* and *Vaccinium* spp., whereas *Sphagnum magellanicum*, *S. capillifolium* and *S. fallax* were the dominant peat moss species (Gavazov *et al.*, 2016). Peat depth was estimated to be > 1.5 m.

At each site, six paired 40x40 cm plots were selected in midsummer 2013. To study the effect of vascular plants on peat decomposition, we clipped the aboveground biomass of vascular plants in half of the plots (-V treatment) without disturbing the moss layer, and left the belowground roots to decompose until measurements commenced the following year (cf. Ward *et al*., 2009; Kuiper *et al*., 2014). We started the field measurements after one year in order to allow the decomposition of most living roots, in particular the most labile fine roots. Due to the low rate of root decomposition in peatlands (Laiho *et al.*, 2004; Moore *et al.*, 2007), we are aware that root biomass did not completely decompose after one year, but the delay of one year in field measurements after biomass removal is, however, expected to have significantly reduced the belowground carbon allocation and root exudation in clipped plots. Vascular plants were left intact in paired control plots (+V treatment) so that our experimental set-up represents a paired-plot design with three replicates. Individual plots were delimited by 10 cm high quadratic stainless steel frames pushed to c. 5 cm depth in the living moss layer, which served as collars for gas flux measurements (see below). At regular intervals during 2013, all plots were trenched along the collars with a 30-cm long knife to avoid root colonisation. In the -V treatments vascular plant regrowth was regularly clipped in 2013, whereas no or very limited regrowth was observed in 2014. Because our primary aim was to study the biogeochemical role of vascular plants on carbon cycling, we decided to limit any secondary effects associated with vascular plant removal by shading the clipped plots (-V) with a UV-resistant mesh simulating the original vascular plant cover as preliminarily measured by photosynthetically active radiation (PAR) extinction

underneath the canopy (60% and 30% at low and high elevation, respectively). By doing so, the presence of a mesh avoided the desiccation of peat mosses, maintained the natural PAR intensity, and avoided changes in soil microclimate. During gas exchange measurements this mesh was instead used over the chamber to maintain the natural light intensity. Ancillary measurements of soil temperature and soil water content in the clipped and control plots at both elevations confirmed the suitability of this approach (Table S2).

Plant biomass and cover estimations

In each peatland, total aboveground vascular plant biomass was estimated by destructively harvesting five random 25x25 cm quadrats at peak standing biomass in 2013. Vascular plant cover within the experimental plots was estimated non-destructively with the point-intercept method. In brief, a pin was lowered over the vegetation through a 40x40 cm grid with 361 holes and the identity of the first intercepted plant was recorded. Species were attributed to one of the existing five categories: graminoids, shrubs, forbs, *Sphagnum spp.* mosses and standing litter, where the total surface cover equals 100%. Control plots (+V) as well as vascular plant removal plots (-V) had 100% *Sphagnum* cover.

CO_2 flux measurements

In 2014, one year after the start of the vascular plant removal treatment, a series of monthly CO_2 flux measurements were carried out during the snow-free period at each peatland starting in mid-April at 1035 m a.s.l. and in mid-June at 1885 m a.s.l. and lasting through to the end of October. CO_2 fluxes at ecosystem level were measured using a custom made transparent (95% light transmission) Plexiglas chamber (40x40 cm wide, 50 cm high) equipped with a diffusion infrared

gas analyser (GMP343, Vaisala, Finland) and a humidity-temperature probe (HMP57, Vaisala, Finland). Air inside the chamber was mixed with a system of inbuilt computer fans. The chamber had a rubber seal on the bottom and a small capped hole on the top which remained open when the chamber was placed on the permanent stainless-steel collar to avoid pressurisation. Net ecosystem CO_2 exchange (NEE) measurements were done in full light or and were immediately followed by ecosystem respiration (R_{eco}) measurements for which the chamber was darkened with a non-transparent cover. All flux measurements were carried out between 10 am and 12 am local time, ensuring optimal photosynthetic conditions for both *Sphagnum* and vascular plants (Bragazza *et al.*, 2016) with vapour-pressure deficit (VPD) below 1.5 kPa and PAR intensity above the vegetation canopy between 1400 and 2100 μmol m^{-2} s^{-1}. Each measurement lasted 1 minute in order to avoid excessive heat and humidity causing condensation inside the chamber. The CO_2 flux was calculated as a linear change in concentration (ppm), taking into account ambient atmospheric pressure and gas temperature. In this study, negative NEE represents a net CO_2 assimilation by the plant community and the calculated gross ecosystem productivity (GEP) was derived from the difference between R_{eco} and NEE.

Radiocarbon analysis and age interpretation

To determine the seasonal contribution of vascular plant-associated R_{eco}, we sampled respired CO_2 for radiocarbon analysis in both the clipped and unclipped plots in July and at the end of September 2014 (Table S3). We used a passive CO_2 sampling method to determine the radiocarbon signature of ecosystem respiration (Garnett *et al.*, 2009). In brief, specific PVC chambers (10 cm diameter, 10 cm height) connected to a zeolite molecular sieve cartridge (MSC) were gas-tight mounted on collars of similar size pre-installed in 2013 in each plot at 7 cm depth.

Prior to sample collection, the atmospheric CO_2 in the chamber headspace was scrubbed by pumping it at a constant rate (0.5 l min^{-1}) through a soda lime column for 10 min while monitoring the concentration. The chambers were then left in place for 10 days until, based on CO_2 production rates, a sufficient amount of CO_2 (i.e. $\geq$ 3 ml) was passively trapped on the MSCs by diffusion without the use of an external pump. The trapped CO_2 was thermally recovered (425 °C) while purging with high-purity nitrogen gas, converted to graphite by Fe/Zn reduction and analysed by acceleration mass spectrometry (AMS) at the NERC Radiocarbon Facility in Scotland, UK (Garnett & Murray, 2013). Subsamples of CO_2 were measured on a dual inlet stable isotope mass spectrometer (Thermo Fisher Delta V) to determine their $\delta^{13}C$ signature.

In addition, we evaluated the apparent carbon accumulation rate at the two peatlands by splitting one 20-cm long peat core from each site into 5 cm segments. From these segments, vascular plant remnants were removed, after which the carbon content, peat density and peat age were determined (Table S4). After the combustion of these samples in a high-pressure bomb in the presence of oxygen, CO_2 was converted to graphite as above. The peat age was estimated by matching the ^{14}C content with a known record (Levin *et al.*, 2013) of atmospheric $^{14}CO_2$ in order to estimate the date of carbon fixation (Goodsite *et al.*, 2001) according to Cali-Bomb program for post-bomb ^{14}C samples (see Reimer *et al.,* 2004).

Following convention (Stuiver & Polach, 1977), all radiocarbon data were corrected for mass dependent fractionation by normalising to $\delta^{13}C$VPDB values of -25‰ using the measured $\delta^{13}C$ values, and reported as %Modern with reference to the Oxalic Acid international radiocarbon standard. These data (Table S3) were not subjected to further corrections for atmospheric air contamination during chamber enclosure (Czimczik *et al.*, 2006; Natali *et al.*, 2011; Hartley *et al.*, 2012; Hicks Pries *et al.*, 2013) as the fraction of atmospheric CO_2 in the recovered samples

194 proved low and subsequent ^{14}C corrections remained within the AMS measurement uncertainty
195 (± 0.5 %Modern).

196 To distinguish between vascular plant-derived respiration and respiration from peat induced
197 by the presence of vascular plants (i.e. the rhizosphere priming effect), we made a common-
198 practice assumption that vascular plants respire contemporary carbon with a ^{14}C signature
199 identical to the current atmosphere (Subke *et al.*, 2011; Hartley *et al.*, 2012), whereas subsurface
200 peat respires older carbon (Hardie *et al.*, 2007), which has become very likely incorporated
201 during the post-1963 bomb-^{14}C spike at our studied sites (Table S3). Experimental evidence from
202 peatlands dominated by herbaceous vegetation supports this assumption for vascular plant shoots
203 (Czimczik *et al.*, 2006; Hicks Pries *et al.*, 2013), and further indicates only a small contribution
204 of carbon fixed in the preceding year (i.e. up to 0.7 %Modern enrichment) for roots (Hicks Pries
205 *et al.*, 2013, 2015). A sensitivity analysis confirmed that our conclusions were robust regardless
206 of whether we used current year atmospheric ^{14}C values or those from the preceding year. We
207 used data from the nearby Jungfraujoch (53°20′ N, 9°54′ W, 3580 m a.s.l.) long-term atmospheric
208 ^{14}C monitoring station (Levin *et al.*, 2013) to calculate a mean seasonal value (June, July, August
209 and September) for the expected vascular plant-derived ^{14}C signature for the 2014 growing
210 season, which was 102.91 %Modern ^{14}C. Elevation differences between the study sites and the
211 ^{14}C monitoring station at the Jungfraujoch are expected not to affect the ^{14}C values due to
212 atmospheric mixing (Levin *et al*., 2008). To this value, we compared the ^{14}C signature of the
213 vascular plant-associated respiration ($D_{V_plant_associated}$) in our experiment. Following Hardie *et al.*
214 (2009), the latter was calculated using a two pool mixing model:

215 $$D_{V_plant_associated} = (D_{+V} \cdot R_{+V} - D_{-V} \cdot R_{-V})/(R_{+V} - R_{-V})$$

where R represents the rate of ecosystem respiration measured on the day of chamber enclosure and D its ^{14}C signature in plots with (+V) and without (-V) vascular plants. The vascular plant-associated respiration in our experiment consisted of vascular plant-derived respiration and, potentially, of vascular plant-induced peat respiration. A significant deviation in the calculated ^{14}C signature of vascular plant associated respiration from that of the expected vascular plant-derived ^{14}C signature (ambient atmosphere) was interpreted as an extra source of heterotrophic peat respiration in the presence of vascular plants, i.e. the rhizosphere priming effect.

Pore-water sampling and chemical analyses

Representative pore-water samples were collected monthly during May-October 2014 from four permanent microporous (0.20 μm) rhizons (Rhizosphere Research Products, The Netherlands) installed in each plot at the rooting depth, i.e. from 5 to 15 cm below the surface. Concentration of ammonium (NH_4^+) and nitrate (NO_3^-) were obtained colorimetrically on a continuous-flow autoanalyser (SEAL Analytical, Germany), whereas total nitrogen (TN) and dissolved organic carbon (DOC) were determined by combustion on a Shimadzu analyser (TOC-V CPHCTNM-1). In order to characterise the quality of dissolved organic matter (DOM) and its level of humification, lyophilised subsamples were analysed on a Frontier FT–NIR/MIR Spectrometer (PerkinElmer, USA). The recorded spectra (4000 to 400 cm^{-1}) of diamond attenuated total reflectance provide information on the DOM functional groups aliphatics (2943 cm^{-1} region), carboxylic acids and aromatic esters (1720 cm^{-1} region), aromatics (1630 cm^{-1} region), lignins (1510 cm^{-1} region), phenols (1420 cm^{-1} region), and polysaccharides (1090 cm^{-1} region) (Niemeyer *et al.*, 1992; Biester *et al.*, 2014). During peat decomposition, substances enriched in carboxylic, aromatic and phenolic groups accumulate with respect to labile polysaccharides,

239 thereby increasing the specific ratios between these moieties (Biester *et al.*, 2014). Commonly
240 referred to as humification indices, the ratios 2943/1090, 1720/1090, 1630/1090, 1510/1090,
241 1420/1090 can be used as an indication of the level of organic matter decomposition (Broder *et*
242 *al.*, 2012; Hodgkins *et al.*, 2014).
243
244 **Statistical analysis**
245 Data on seasonal CO_2 fluxes and pore-water chemistry were analysed as a paired-plot design for
246 the effect of vascular plant removal in each peatland. The hierarchical structure was coded in
247 R3.3 (R Core Team, 2016) as a linear mixed-effects model using the *nlme* package (Pinheiro *et*
248 *al.*, 2016), accounting for the spatial proximity of +V (control) and -V (clipped) pairs and the
249 repeated measurements in individual plots. Assumptions of normality and homoscedasticity of
250 the residuals in all final models were verified visually using diagnostic plots, and the simplest
251 models were retained by pooling non-significant interactions with the error term. Comparisons
252 between the radiocarbon signature of the atmosphere and the estimated vascular plant-associated
253 CO_2 were done in R using One Sample t-tests for each site and sampling date.
254
255 **RESULTS**
256 The main hydrological (water-table depth) and hydro-chemical (water pH and electrical
257 conductivity) parameters were comparable between the two peatlands and overall typical of
258 ombrotrophic peatlands, i.e. rain-fed bogs (Table 1). The main differences between the two sites
259 were related to climatic conditions and abundance of vascular plants, with characteristically
260 higher air temperature, lower precipitation and higher shrub biomass at low elevation (Table 1,
261 Table S1). Because the cover of peat mosses at plot level did not differ between the two sites

(100% at both sites), the study sites can be regarded as a natural climate change experiment where the natural climatic gradient resulted in similar plant community composition, but with different abundance of vascular plants in response to soil microclimate (Table 1, Table S2).

Overall, the net ecosystem exchange of atmospheric carbon (i.e., NEE) was weaker (i.e. smaller sink capacity) at low elevation with warmer climatic conditions ($F_{1,4}$ = 15.5, P = 0.017) despite the larger vascular plant biomass (Fig. 1a). Nevertheless, in both peatlands the presence of vascular plants (+V treatment) increased ($F_{1,35}$ = 19.4, P < 0.001) the net CO_2 assimilation by c. 50% compared to the treatment with *Sphagnum* mosses alone (-V treatment) (Fig. 1a). Furthermore, at low elevation the absence of vascular plants prevented a net assimilation of atmospheric carbon during most of the growing season (Fig. 1a).

During the peak of the growing season, vascular plants contributed to about 50% to gross photosynthesis at both elevations (Fig. 1b) as indicated by the two-fold reduction of potential gross ecosystem productivity (GEP) upon vascular plant removal ($F_{1,35}$ = 50.2, P < 0.001). Although vascular plant biomass was significantly larger at low elevation (Table 1), the GEP was similar at both sites in the presence of vascular plants (+V). In the absence of vascular plants (-V), GEP of *Sphagnum* mosses was also comparable between the two sites (Fig. 1b).

Overall, ecosystem respiration (R_{eco}) was slightly larger at low elevation as compared to high elevation site ($F_{1,4}$ = 6.4, P = 0.064) and at both sites the presence of vascular plants increased R_{eco} ($F_{1,35}$ = 46.9, P < 0.001) (Fig. 1c). By taking into account the CO_2 flux and the corresponding ^{14}C signature in plots with and without vascular plants, the two-pool mixing model revealed that late in the growing season the vascular plant-associated respiration was more enriched in bomb-^{14}C than would be expected from autotrophic contributions alone at both low ($t_{1,2}$ = 8.8, P = 0.006) and high ($t_{1,2}$ = 2.7, P = 0.053) elevation (Fig. 2). An enrichment in bomb-

285 ^{14}C likely occurred also during the peak of the growing season in July (Fig. 2); however, it was
286 masked by larger variability at both low ($t_{1,2}$ = 1.4, P = 0.153) and high elevation ($t_{1,2}$ = 1.9, P =
287 0.096).

288 On the basis of pore-water chemistry, the peatland at low elevation was characterized by a c.
289 30% greater concentration of dissolved organic carbon (DOC) (Table 1). Furthermore, the FT-IR
290 spectroscopy demonstrated that the presence of vascular plants (+V) was associated with a
291 consistently higher humification of dissolved organic matter in both peatlands. This was
292 indicated by higher concentrations of aliphatic, carboxylic, aromatic, lignin, and phenolic
293 compounds in proportion to more labile polysaccharides (Fig. 3).

294

295 **DISCUSSION**

296 Our net ecosystem exchange (NEE) measurements under optimal conditions and during the peak
297 of diurnal photosynthetic activity provide an objective assessment of the potential contribution of
298 vascular plants and *Sphagnum* mosses to the exchange of atmospheric CO_2 in the two contrasting
299 peatlands (Bahn *et al.*, 2009; Bragazza *et al.*, 2016). The NEE results demonstrate that the
300 presence of vascular plants is crucial to maintain high levels of net CO_2 assimilation in the two
301 peatlands during the growing season (Laine *et al.*, 2012; Ward *et al.*, 2013; Kuiper *et al.*, 2014).
302 *Sphagnum* mosses alone were much less efficient in offsetting ecosystem respiratory CO_2 losses
303 under warmer conditions. Concurrently, gross ecosystem productivity (GEP) in both peatlands
304 was much higher in the presence of vascular plants, in accordance with the higher photosynthetic
305 efficiency of vascular plants compared to mosses (Ward *et al.*, 2009; Armstrong *et al.*, 2015).
306 Despite the larger aboveground plant biomass at lower elevation, GEP was not significantly
307 different between the two peatlands, a result that can be at least partly explained by a larger

abundance of shrubs with a greater portion of ligneous, non-photosynthetic tissues at low elevation (Table 1; Fig. S1) (Bubier *et al.*, 2003; Leppälä *et al.*, 2008; Juutinen *et al.*, 2010). On the basis of our field measurements, *Sphagnum* mosses in the two peatlands contributed equally to GEP per surface area, indicating that under suitable conditions of temperature and moisture the photosynthetic potential was the same at both elevations even if the annual productivity can be different (Bragazza *et al.*, 2013). Indeed, albeit a longer growing season (Fig. 1), both vascular plants and *Sphagnum* mosses are likely to experience more limiting photosynthetic conditions at lower elevation due to higher VPD values (Table 1).

The overall greater R_{eco} in the presence of vascular plants, particularly at low elevation, is likely due to a higher contribution of autotrophic respiration, in line with: the larger vascular plant biomass (Ward *et al.*, 2013; Kuiper *et al.*, 2014; Hicks Pries *et al.*, 2015), the corresponding larger biomass of decomposing roots (Murphy *et al.*, 2009), as well as to an enhancement of heterotrophic respiration, i.e. a boosting of microbial metabolism. The latter can be directly stimulated by the improved soil physical conditions due to warmer climate (Updegraff *et al.*, 2001; Dorrepaal *et al.*, 2009; Conant *et al.*, 2011; Philben *et al.*, 2014) or indirectly promoted by vascular plants through the rhizosphere priming. The two-pool mixing model, taking into account the CO_2 efflux and the corresponding ^{14}C signature in plots with and without vascular plants at each peatland, shows a consistent enrichment of vascular plant-associated respiration with older carbon, a result that clearly indicates a stimulation of heterotrophic peat decomposition through the rhizosphere priming effect (Hardie *et al.*, 2009; Basiliko *et al.*, 2012; Walker *et al.*, 2016). Although we cannot exclude a contribution of residual decomposing roots to the priming (even after one year of decomposition), if this should take place in the clipped plots it means that the

differences in the ^{14}C enrichment with the control plots would be still larger in total absence of roots in the peat.

A sustained expression of the rhizosphere priming towards the end of the growing season is intriguing because it indicates that the priming can still be active beyond the plant growing season, i.e. when soil and air temperatures as well as GEP already decline (Fig. 1, Table S2). We interpret this apparent temporal asynchrony between aboveground plant productivity and belowground microbial decomposition as result of: i) the low thermal diffusivity of peat that maintained favourable soil temperatures later into the growing season (Table S2), ii) the preferential allocation of carbon resources by vascular plants to their roots well beyond their aboveground senescence (Abramoff & Finzi, 2015; Blume-Werry *et al.*, 2016), and iii) the leaching from fresh leaf litter (Singh *et al.*, 2014) providing soil microbes with labile carbon substrates to access older organic matter (Qiao *et al.*, 2014).

On the basis of FT-IR spectroscopy, at both studied sites there was a higher humification degree of dissolved organic matter in plots with intact vascular plants (Fig. 3), a result that seems to reflect an enhanced microbial metabolism (Glatzel *et al.*, 2003; Höll *et al.*, 2009; Ward *et al.*, 2013; Lou *et al.*, 2014; Dieleman *et al.*, 2016). The removal of vascular plants is indeed expected to reduce the availability of more labile, root-mediated carbon (Gogo *et al.*, 2011) that is used by microbes for synthesising extracellular enzymes (Robroek *et al.*, 2016). Additionally, we observe that warmer climatic conditions and larger vascular plant biomass are ultimately associated with a larger release of dissolved organic carbon (DOC) in the peat soil at low elevation (Table 1). This latter result points to the synergetic role of climate and vegetation in increasing the production and release of DOC from peatlands (Neff & Hooper, 2002; Frey & Smith, 2005; Ward *et al.*, 2013; Kane *et al.*, 2014).

On the basis of the ^{14}C signature in the subsurface peat (Table 1), the estimated age of top 20 cm peat, particularly for the low elevation site, was in line with other studies (see e.g. Shotyk *et al*., 1997) suggesting a relatively recent peat accumulation, i.e. primarily after the bomb- ^{14}C peak of 1963. We conclude that the carbon released by the priming effect was only a few decades old (< 20 years) and stored above the mean water-table depth (Table 1). This observation highlights the importance of water table in protecting peat from microbial decomposition (Ise *et al.*, 2008), but also indicates the potential vulnerability of peat carbon if hydrological feedbacks to climate change increase soil oxygenation (Waddington *et al.*, 2015) and, consequently, promote the spreading of vascular plants (Dieleman *et al.*, 2015; Potvin *et al.*, 2015). The apparent rate of carbon accumulation in the peat layers above the mean-water table depth approximated c. 90 g C m^{-2} y^{-1} for the low elevation site and c. 154 g C m^{-2} y^{-1} for the high elevation site over a reference period of 26-30 years for both sites, a result suggesting a lower carbon sink capacity of peatlands at the lower end of their altitudinal distribution (Millar *et al.*, 2017). The effective annual contribution of the rhizosphere priming to the observed difference in carbon accumulation rate in relation to the dominant vascular plant functional types and their symbiotic microorganisms remains an open question that deserves further attention (Gavazov *et al*., 2016; Walker *et al*., 2016; Sulman *et al*., 2017).

Our CO_2 exchange measurements, whilst covering only a single growing season, show that the presence of vascular plants is crucial to sustain high potential levels of net atmospheric carbon assimilation in peatlands, particularly with warmer climate. Differently, *Sphagnum* mosses alone could not keep pace with the observed higher ecosystem respiratory C-losses with warmer climate. A sustained temporal expression of the rhizosphere priming effect, although deserving further investigation (Luo *et al*., 2016), suggests that the decomposition of older peat can be

promoted even beyond the plant growing season, so affecting the humification of peat and loss of C in both gaseous and dissolved form. We argue that to accurately predict the future capacity of peatlands to act as atmospheric carbon sinks the synergetic interactions among vegetation dynamics, plant phenology and soil microbes must be taken into account, particularly if the rhizosphere priming effect can be further stimulated in warmer soils (Zhu & Cheng, 2011), thereby exerting a positive feedback to carbon emissions from organic rich soils.

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TABLE 1 Geographical location, climatic conditions for the year 2014 and the average for the period 2005-2013 (in brackets), cumulative hours of vapour-pressure deficit (VPD) and water-table depth during plant growing season 2014, vascular plant biomass and surface cover (%), pore-water chemistry, and estimated age of surface peat (with corresponding ^{14}C signature) at the two study sites. Aboveground plant biomass is the mean of 5 replicates for each site. Water table depth is the seasonal mean of continuous measurements collected in one representative piezometer during the plant growing season at each site. Plant cover estimates are mean (± 1 SE) of 3 replicates for each site. Pore-water chemistry is the seasonal mean (± 1 SE) of 3 replicates for each site as measured in the control plots where vascular plants were not clipped (+V treatment). Different superscripts indicate significant differences between the peatlands ($P < 0.05$). The age of the peat was calculated from a reference dataset of atmospheric ^{14}C measurements carried out at the Jungfraujoch station and refers to years before 2014.

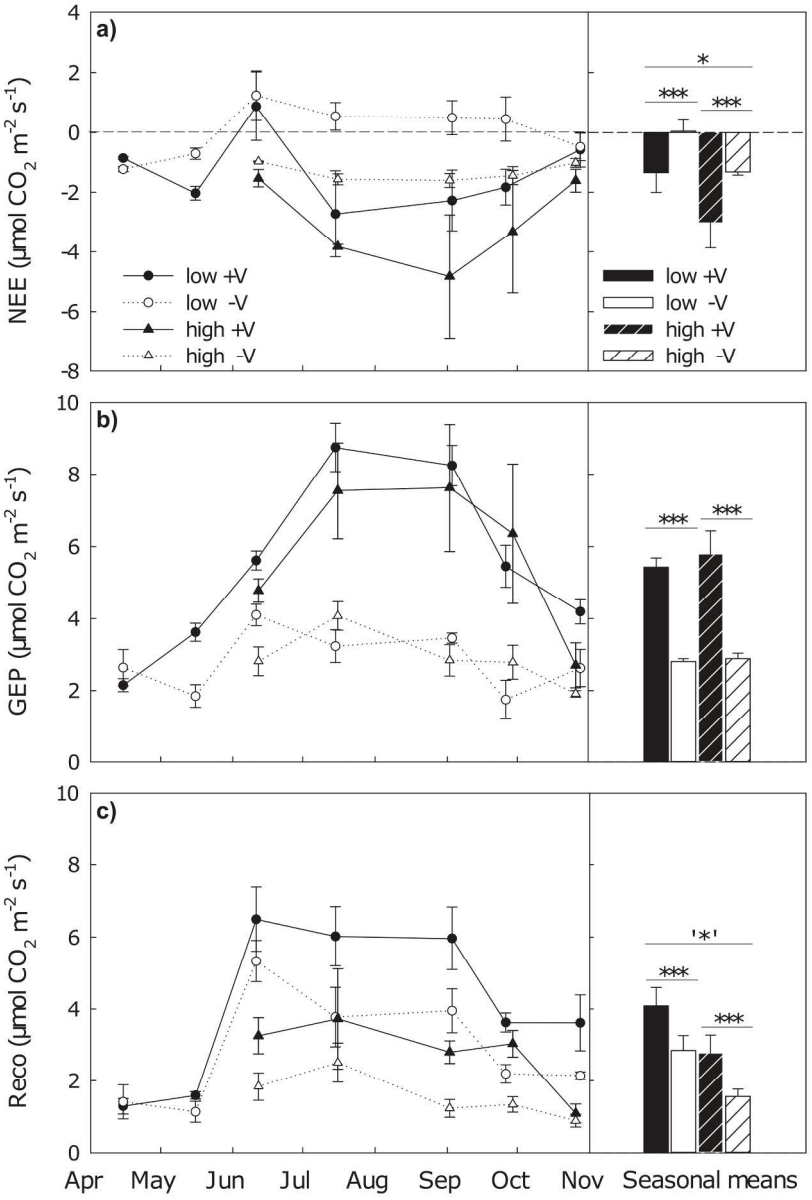
	Praz Rodet	Hochrajen
Elevation (m a.s.l.)	1035	1885
Latitude and longitude	46°33'N, 6°10'E	46°36'N, 7°58'E
Mean annual air temperature (°C)	7.0 (6.2)	3.7 (3.3)
Mean annual precipitation (mm)	1219 (1264)	1427 (1372)
VPD > 1.5 kPa (hours)	150	53
Mean water-table depth (cm)	-17.8	-15.6
Total aboveground vascular plant biomass (g m^{-2})	$160^{a} \pm 21$	$74^{b} \pm 7$
Total vascular plant cover (%)	$63.0^{a} \pm 2.0$	$35.4^{b} \pm 5.3$
Graminoids (%)	$26.5^{a} \pm 3.3$	$19.0^{a} \pm 3.4$
Shrubs (%)	$20.0^{a} \pm 2.6$	$8.3^{b} \pm 1.8$
Forbs (%)	$1.2^{a} \pm 0.5$	$1.8^{a} \pm 1.8$
Standing litter (%)	$15.\ 2^{a} \pm 1.4$	$6.3^{b} \pm 1.9$
Total moss cover (%)	$100^{a} \pm 0.0$	$100^{a} \pm 0.0$
pH	$4.25^{a} \pm 0.02$	$4.37^{a} \pm 0.15$
Conductivity (µS cm^{-1})	$31.03^{a} \pm 0.64$	$27.81^{a} \pm 7.34$
Total N (mg l^{-1})	$0.39^{a} \pm 0.03$	$0.30^{b} \pm 0.02$
NH_4^+ (mg l^{-1})	$0.018^{a} \pm 0.003$	$0.007^{b} \pm 0.002$
NO_3^- (mg l^{-1})	$0.034^{a} \pm 0.002$	$0.032^{a} \pm 0.001$
DOC (mg l^{-1})	$22.14^{a} \pm 1.12$	$16.57^{b} \pm 1.53$
Age at 5-10 cm (years / %Mod$^{14}C \pm 1\sigma$)	16 / 110.23 ± 0.48	1 / 103.41 ± 0.47
Age at 10-15 cm (years / %Mod$^{14}C \pm 1\sigma$)	30 / 120.75 ± 0.53	16 / 110.01 ± 0.48
Age at 15-20 cm (years / %Mod$^{14}C \pm 1\sigma$)	40 / 139.28 ± 0.61	26 / 117.12 ± 0.51

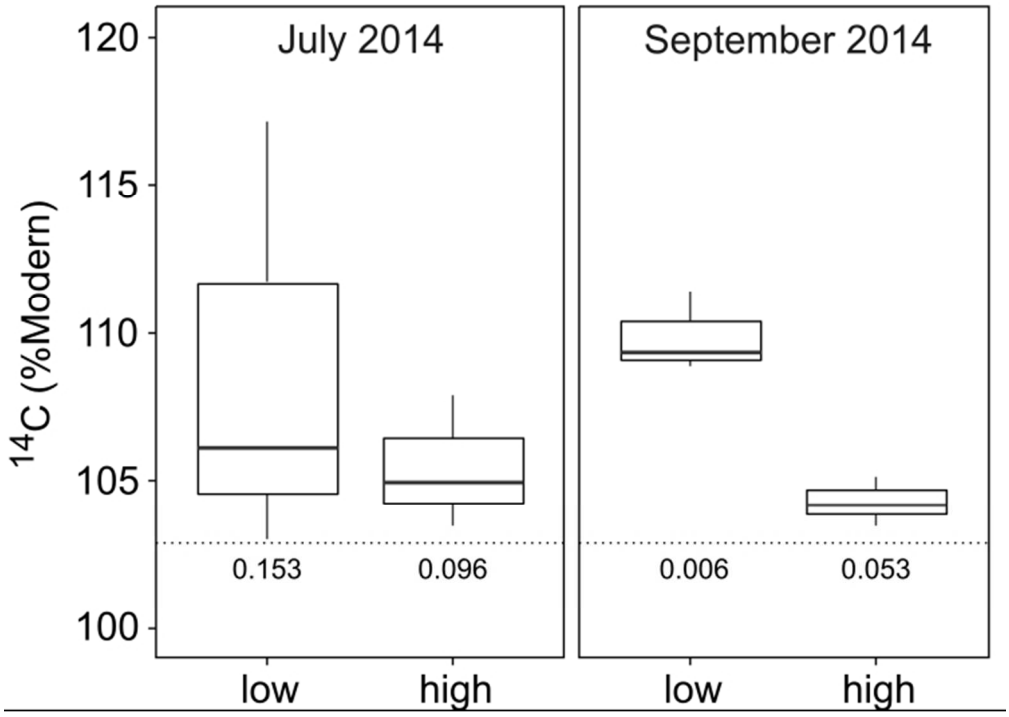
FIGURE CAPTIONS

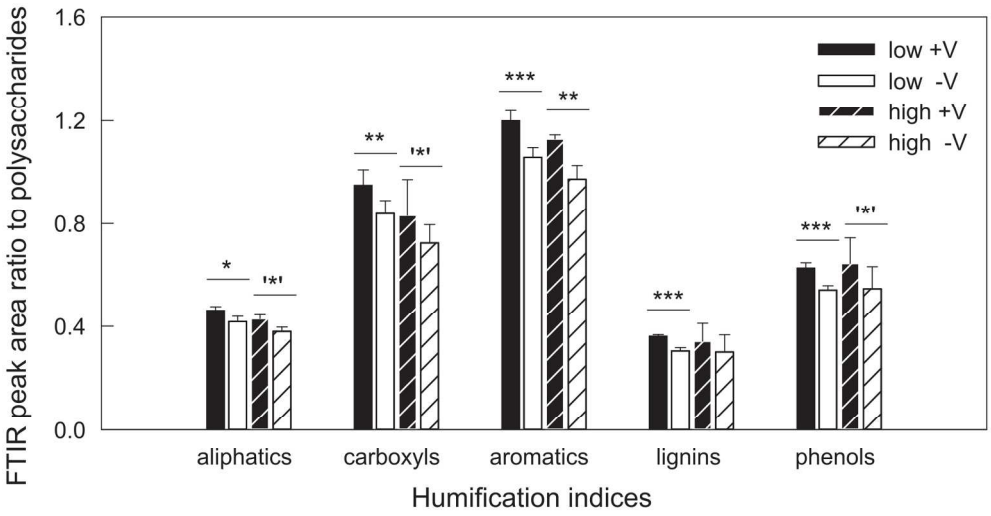
Fig. 1 Seasonal dynamics of ecosystem CO_2 fluxes in relation to the presence or absence of vascular plants in two peatlands at different elevations. (a) Net ecosystem exchange (NEE), (b) Gross ecosystem productivity (GEP), (c) Ecosystem respiration (R_{eco}). The two peatlands were located at low (1035 m a.s.l.) and high elevation (1885 m a.s.l.) and two treatments were applied, i.e. mosses plus vascular plants present (+V, controls) or removal of vascular plants by clipping (-V, *Sphagnum* mosses alone). Panels on the left show the seasonal dynamics of mean values (± 1 SE, $n = 3$), whereas those on the right show the overall seasonal means (± 1 SE, $n = 3$). Asterisks indicate significant differences of mean CO_2 fluxes between treatments at each site and between elevations ('*' = $P < 0.1$; * = $P < 0.05$; *** = $P < 0.001$). Negative values of NEE indicate a net assimilation of atmospheric CO_2.

Fig. 2 ^{14}C content of ecosystem respired CO_2 associated with the presence of vascular plants in two peatlands at low and high elevations (1035 and 1885 m a.s.l., respectively) at peak biomass (July) and late in the growing season (end of September). Median and range ($n = 3$) of respired ^{14}C-CO_2 associated with the presence of vascular plants (DV_plant_associated). Dotted line indicates the mean atmospheric ^{14}C-CO_2 signature (102.91 %Modern) as measured in June, July, August and September 2014 at the Jungfraujoch atmospheric research station. Numbers beneath the dotted line are *P*-values from t-tests for differences of each date and elevation to this reference line. Significant differences ($P < 0.05$) are interpreted as a signal of plant-induced heterotrophic respiration of peat carbon through the rhizosphere priming effect.

Fig. 3 Mean seasonal values (± 1 SE, $n = 3$) of humification indices of dissolved organic matter based on FT-IR spectra. Pore-water samples were collected monthly from May through October 2014 in the two peatlands at low and high elevations (1035 and 1885 m a.s.l., respectively) in relation to the presence (+V) or absence (-V) of vascular plants. The selected functional groups are: aliphatics (2943 cm^{-1} region), carboxylic acids and aromatic esters (1720 cm^{-1} region), aromatics (1630 cm^{-1} region), lignins (1510 cm^{-1} region), phenols (1420 cm^{-1} region) and they are expressed as a ratio to polysaccharides (1090 cm^{-1} region). Significant differences between treatments are indicated with asterisks ('*' = $P < 0.1$, * = $P < 0.05$, ** = $P < 0.01$; *** = $P < 0.001$), whereas no significant differences were observed between the two sites.


a)
b)
c)
NEE (µmol CO2 m-2 s-1)
GEP (µmol CO2 m-2 s-1)
Reco (µmol CO2 m-2 s-1)
low +V
low -V
high +V
high -V
*
***
***
'*'
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Seasonal means


July 2014
September 2014
120
115
110
105
100
^{14}C (%Modern)
0.153
0.096
0.006
0.053
low
high
low
high


FTIR peak area ratio to polysaccharides
1.6
1.2
0.8
0.4
0.0
low +V
low -V
high +V
high -V
*
'*'
**
'*'
***
**
***
'*'
aliphatics
carboxyls
aromatics
lignins
phenols
Humification indices