



HAL
open science

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

Konstantin Gavazov, Remy Albrecht, Alexandre Buttler, Ellen Dorrepaal, Mark Garnett, Sébastien Gogo, Frank Hagedorn, Robert T.E. Mills, Bjorn J.M. Robroek, Luca Bragazza

► To cite this version:

Konstantin Gavazov, Remy Albrecht, Alexandre Buttler, Ellen Dorrepaal, Mark Garnett, et al.. Vascular plant-mediated controls on atmospheric carbon assimilation and peat carbon decomposition under climate change. *Global Change Biology*, 2018, 24 (9), pp.3911-3921. 10.1111/gcb.14140 . insu-01744835

HAL Id: insu-01744835

<https://insu.hal.science/insu-01744835v1>

Submitted on 28 Nov 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3

4 Running head: Vascular plants and peat carbon cycling

5

6 Konstantin Gavazov^{1,2,3}, Remy Albrecht^{1,2}, Alexandre Buttler^{1,2,4}, Ellen Dorrepaal³, Mark H.

7 Garnett⁵, Sebastien Gogo^{6,7,8}, Frank Hagedorn⁹, Robert T.E. Mills^{1,2,10}, Bjorn J.M. Robroek^{1,2,11},

8 Luca Bragazza^{1,2,12}

9

10 ¹Swiss Federal Institute for Forest, Snow and Landscape Research, WSL Site Lausanne, Station
11 2, 1015 Lausanne, Switzerland

12 ²Ecole Polytechnique Fédérale de Lausanne EPFL, School of Architecture, Civil and
13 Environmental Engineering ENAC, Laboratory of ecological systems ECOS, Station 2, 1015
14 Lausanne, Switzerland

15 ³Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå
16 University, 98107 Abisko, Sweden

17 ⁴Laboratoire de Chrono-Environnement, UMR CNRS 6249, UFR des Sciences et Techniques,
18 Université de Franche-Comté, Besançon 25030, France

19 ⁵NERC Radiocarbon Facility (East Kilbride), Scottish Enterprise Technology Park, Rankine
20 Avenue, East Kilbride, Scotland, G75 0QF, United Kingdom

21 ⁶Université d'Orléans, ISTO, UMR 7327, 45071 Orléans, France

22 ⁷CNRS, ISTO, UMR 7327, 45071 Orléans, France

23 ⁸BRGM, ISTO, UMR 7327, BP 36009, 45060 Orléans, France

24 ⁹Swiss Federal Institute for Forest, Snow and Landscape, Research, WSL Site Birmensdorf,
25 8903, Birmensdorf, Switzerland

26 ¹⁰Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, United Kingdom

27 ¹¹Biological Sciences, University of Southampton, Southampton SO17 1BJ, United Kingdom

28 ¹²Department of Life Science and Biotechnologies, University of Ferrara, Corso Ercole I d'Este
29 32, I-44121 Ferrara, Italy

30

31 **Correspondence**

32 Luca Bragazza, Tel: +39 0532 293773, Email: luca.bragazza@unife.it

33

34 **KEYWORDS**

35 climate warming, decomposition, ecosystem respiration, net ecosystem CO₂ exchange, peatlands,
36 rhizosphere priming, vascular plant biomass, elevation gradient

37

38 **Paper type: PRIMARY RESEARCH ARTICLE**

39 **Abstract**

40 Climate change can alter peatland plant community composition by promoting the growth of
41 vascular plants. How such vegetation change affects peatland carbon dynamics remains,
42 however, unclear. In order to assess the effect of vegetation change on carbon uptake and release,
43 we performed a vascular-plant removal experiment in two *Sphagnum*-dominated peatlands that
44 represent contrasting stages of natural vegetation succession along a climatic gradient. Periodic
45 measurements of net ecosystem CO₂ exchange revealed that vascular plants play a crucial role in
46 assuring the potential for net carbon uptake, particularly with a warmer climate. The presence of
47 vascular plants, however, also increased ecosystem respiration, and by using the seasonal
48 variation of respired CO₂ radiocarbon (bomb-¹⁴C) signature we demonstrate an enhanced
49 heterotrophic decomposition of peat carbon due to rhizosphere priming. The observed
50 rhizosphere priming of peat carbon decomposition was matched by more advanced humification
51 of dissolved organic matter, which remained apparent beyond the plant growing season. Our
52 results underline the relevance of rhizosphere priming in peatlands, especially when assessing the
53 future carbon sink function of peatlands undergoing a shift in vegetation community composition
54 in association with climate change.

55

56 INTRODUCTION

57 Peatlands are formed under climatic, hydrological and biological conditions that suppress the
58 decomposition of plant litter, resulting in the accumulation of organic matter as peat. The
59 imbalance between litter production and decomposition makes peatlands effective long-term
60 sinks of atmospheric carbon (Yu, 2012). Indeed, despite a distribution limited to c. 3% of the
61 Earth's land surface, peatlands contain c. 30% of its soil carbon (Yu, 2012). In northern
62 peatlands, *Sphagnum* mosses play a crucial role in peat accumulation due to the production of
63 litter particularly resistant to microbial decomposition (Hájek *et al.*, 2011). However, alteration of
64 the hydrological balance (Talbot *et al.*, 2014; Munir *et al.*, 2015), increase in nitrogen availability
65 (Bubier *et al.*, 2007; Juutinen *et al.*, 2010) and, more specifically, climate warming (Weltzin *et*
66 *al.*, 2000; Dieleman *et al.*, 2015) can promote the growth and cover of vascular plants in
67 peatlands. Such increase in the abundance of vascular plants can potentially reduce the
68 productivity of *Sphagnum* mosses due to, for example, lower light availability (Chong *et al.*,
69 2012) and increasing evapotranspiration (Hirano *et al.*, 2016). In addition, considering that the
70 decomposition rate of vascular plant litter is much faster than that of *Sphagnum* mosses
71 (Dorrepaal, 2007), it is crucial to clarify the role of a higher vascular plant biomass, particularly
72 with a warmer climate, with reference to the capability of the system to act as carbon sink
73 (Breeuwer *et al.*, 2010; Ward *et al.*, 2013; Wang *et al.*, 2015).

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

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

83 To investigate the role of vascular plants in the seasonal net assimilation of atmospheric
84 carbon and in the decomposition of peat carbon under contrasting climatic conditions, we
85 performed a vascular plant-removal experiment in two *Sphagnum*-dominated peatlands that were
86 located at different elevations and thereby naturally differed in mean annual temperature,
87 growing season length and vascular plant abundance (Table 1). As such, the comparison of our
88 study sites should be interpreted as a space-for-time substitution (Blois *et al.*, 2013), whereby the
89 low elevation peatland represents the ecosystem state resulting from a natural response of
90 vegetation to warmer climate compared to the upslope site (Klaus, 2007). During a full growing
91 season, we periodically measured the net ecosystem CO₂ exchange (NEE), the ecosystem
92 respiration (R_{eco}) and its radiocarbon signature, and the humification degree of dissolved organic
93 matter in order to: 1) assess the role of vascular plants in assimilation of atmospheric CO₂
94 compared to *Sphagnum* mosses under contrasting climatic conditions; and 2) detect any temporal
95 link between the presence of vascular plants and enhanced decomposition of peat through
96 rhizosphere priming and the associated carbon release into both the atmosphere and pore water.

97

98 **MATERIAL AND METHODS**

99 **Study sites and experimental design**

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

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

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

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

131

132 **Plant biomass and cover estimations**

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

141

142 **CO₂ flux measurements**

143 In 2014, one year after the start of the vascular plant removal treatment, a series of monthly CO₂
144 flux measurements were carried out during the snow-free period at each peatland starting in mid-
145 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.
146 CO₂ fluxes at ecosystem level were measured using a custom made transparent (95% light
147 transmission) Plexiglas chamber (40x40 cm wide, 50 cm high) equipped with a diffusion infrared

148 gas analyser (GMP343, Vaisala, Finland) and a humidity-temperature probe (HMP57, Vaisala,
149 Finland). Air inside the chamber was mixed with a system of inbuilt computer fans. The chamber
150 had a rubber seal on the bottom and a small capped hole on the top which remained open when
151 the chamber was placed on the permanent stainless-steel collar to avoid pressurisation. Net
152 ecosystem CO₂ exchange (NEE) measurements were done in full light or and were immediately
153 followed by ecosystem respiration (R_{eco}) measurements for which the chamber was darkened
154 with a non-transparent cover. All flux measurements were carried out between 10 am and 12 am
155 local time, ensuring optimal photosynthetic conditions for both *Sphagnum* and vascular plants
156 (Bragazza *et al.*, 2016) with vapour-pressure deficit (VPD) below 1.5 kPa and PAR intensity
157 above the vegetation canopy between 1400 and 2100 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Each measurement lasted 1
158 minute in order to avoid excessive heat and humidity causing condensation inside the chamber.
159 The CO₂ flux was calculated as a linear change in concentration (ppm), taking into account
160 ambient atmospheric pressure and gas temperature. In this study, negative NEE represents a net
161 CO₂ assimilation by the plant community and the calculated gross ecosystem productivity (GEP)
162 was derived from the difference between R_{eco} and NEE.

163

164 **Radiocarbon analysis and age interpretation**

165 To determine the seasonal contribution of vascular plant-associated R_{eco}, we sampled respired
166 CO₂ for radiocarbon analysis in both the clipped and unclipped plots in July and at the end of
167 September 2014 (Table S3). We used a passive CO₂ sampling method to determine the
168 radiocarbon signature of ecosystem respiration (Garnett *et al.*, 2009). In brief, specific PVC
169 chambers (10 cm diameter, 10 cm height) connected to a zeolite molecular sieve cartridge (MSC)
170 were gas-tight mounted on collars of similar size pre-installed in 2013 in each plot at 7 cm depth.

171 Prior to sample collection, the atmospheric CO₂ in the chamber headspace was scrubbed by
172 pumping it at a constant rate (0.5 l min⁻¹) through a soda lime column for 10 min while
173 monitoring the concentration. The chambers were then left in place for 10 days until, based on
174 CO₂ production rates, a sufficient amount of CO₂ (i.e. ≥ 3 ml) was passively trapped on the
175 MSCs by diffusion without the use of an external pump. The trapped CO₂ was thermally
176 recovered (425 °C) while purging with high-purity nitrogen gas, converted to graphite by Fe/Zn
177 reduction and analysed by acceleration mass spectrometry (AMS) at the NERC Radiocarbon
178 Facility in Scotland, UK (Garnett & Murray, 2013). Subsamples of CO₂ were measured on a dual
179 inlet stable isotope mass spectrometer (Thermo Fisher Delta V) to determine their δ¹³C signature.

180 In addition, we evaluated the apparent carbon accumulation rate at the two peatlands by
181 splitting one 20-cm long peat core from each site into 5 cm segments. From these segments,
182 vascular plant remnants were removed, after which the carbon content, peat density and peat age
183 were determined (Table S4). After the combustion of these samples in a high-pressure bomb in
184 the presence of oxygen, CO₂ was converted to graphite as above. The peat age was estimated by
185 matching the ¹⁴C content with a known record (Levin *et al.*, 2013) of atmospheric ¹⁴CO₂ in order
186 to estimate the date of carbon fixation (Goodsite *et al.*, 2001) according to Cali-Bomb program
187 for post-bomb ¹⁴C samples (see Reimer *et al.*, 2004).

188 Following convention (Stuiver & Polach, 1977), all radiocarbon data were corrected for mass
189 dependent fractionation by normalising to δ¹³CVPDB values of -25‰ using the measured δ¹³C
190 values, and reported as %Modern with reference to the Oxalic Acid international radiocarbon
191 standard. These data (Table S3) were not subjected to further corrections for atmospheric air
192 contamination during chamber enclosure (Czimczik *et al.*, 2006; Natali *et al.*, 2011; Hartley *et*
193 *al.*, 2012; Hicks Pries *et al.*, 2013) as the fraction of atmospheric CO₂ in the recovered samples

194 proved low and subsequent ^{14}C corrections remained within the AMS measurement uncertainty
195 ($\pm 0.5\%$ 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 respire 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 ($D_{\text{V_plant_associated}}$) in our experiment. Following Hardie *et al.*
214 (2009), the latter was calculated using a two pool mixing model:

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

216 where R represents the rate of ecosystem respiration measured on the day of chamber enclosure
217 and D its ^{14}C signature in plots with (+V) and without (-V) vascular plants. The vascular plant-
218 associated respiration in our experiment consisted of vascular plant-derived respiration and,
219 potentially, of vascular plant-induced peat respiration. A significant deviation in the calculated
220 ^{14}C signature of vascular plant associated respiration from that of the expected vascular plant-
221 derived ^{14}C signature (ambient atmosphere) was interpreted as an extra source of heterotrophic
222 peat respiration in the presence of vascular plants, i.e. the rhizosphere priming effect.

223

224 **Pore-water sampling and chemical analyses**

225 Representative pore-water samples were collected monthly during May-October 2014 from four
226 permanent microporous (0.20 μm) rhizons (Rhizosphere Research Products, The Netherlands)
227 installed in each plot at the rooting depth, i.e. from 5 to 15 cm below the surface. Concentration
228 of ammonium (NH_4^+) and nitrate (NO_3^-) were obtained colorimetrically on a continuous-flow
229 autoanalyser (SEAL Analytical, Germany), whereas total nitrogen (TN) and dissolved organic
230 carbon (DOC) were determined by combustion on a Shimadzu analyser (TOC-V CPHCTNM-1).
231 In order to characterise the quality of dissolved organic matter (DOM) and its level of
232 humification, lyophilised subsamples were analysed on a Frontier FT-NIR/MIR Spectrometer
233 (PerkinElmer, USA). The recorded spectra (4000 to 400 cm^{-1}) of diamond attenuated total
234 reflectance provide information on the DOM functional groups aliphatics (2943 cm^{-1} region),
235 carboxylic acids and aromatic esters (1720 cm^{-1} region), aromatics (1630 cm^{-1} region), lignins
236 (1510 cm^{-1} region), phenols (1420 cm^{-1} region), and polysaccharides (1090 cm^{-1} region)
237 (Niemeyer *et al.*, 1992; Biester *et al.*, 2014). During peat decomposition, substances enriched in
238 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 CO₂ 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 CO₂ 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

262 (100% at both sites), the study sites can be regarded as a natural climate change experiment
263 where the natural climatic gradient resulted in similar plant community composition, but with
264 different abundance of vascular plants in response to soil microclimate (Table 1, Table S2).

265 Overall, the net ecosystem exchange of atmospheric carbon (i.e., NEE) was weaker (i.e.
266 smaller sink capacity) at low elevation with warmer climatic conditions ($F_{1,4} = 15.5$, $P = 0.017$)
267 despite the larger vascular plant biomass (Fig. 1a). Nevertheless, in both peatlands the presence
268 of vascular plants (+V treatment) increased ($F_{1,35} = 19.4$, $P < 0.001$) the net CO₂ assimilation by
269 c. 50% compared to the treatment with *Sphagnum* mosses alone (-V treatment) (Fig. 1a).
270 Furthermore, at low elevation the absence of vascular plants prevented a net assimilation of
271 atmospheric carbon during most of the growing season (Fig. 1a).

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

278 Overall, ecosystem respiration (R_{eco}) was slightly larger at low elevation as compared to high
279 elevation site ($F_{1,4} = 6.4$, $P = 0.064$) and at both sites the presence of vascular plants increased
280 R_{eco} ($F_{1,35} = 46.9$, $P < 0.001$) (Fig. 1c). By taking into account the CO₂ flux and the
281 corresponding ¹⁴C signature in plots with and without vascular plants, the two-pool mixing model
282 revealed that late in the growing season the vascular plant-associated respiration was more
283 enriched in bomb-¹⁴C than would be expected from autotrophic contributions alone at both low
284 ($t_{1,2} = 8.8$, $P = 0.006$) 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

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

316 The overall greater R_{eco} in the presence of vascular plants, particularly at low elevation, is
317 likely due to a higher contribution of autotrophic respiration, in line with: the larger vascular
318 plant biomass (Ward *et al.*, 2013; Kuiper *et al.*, 2014; Hicks Pries *et al.*, 2015), the corresponding
319 larger biomass of decomposing roots (Murphy *et al.*, 2009), as well as to an enhancement of
320 heterotrophic respiration, i.e. a boosting of microbial metabolism. The latter can be directly
321 stimulated by the improved soil physical conditions due to warmer climate (Updegraff *et al.*,
322 2001; Dorrepaal *et al.*, 2009; Conant *et al.*, 2011; Philben *et al.*, 2014) or indirectly promoted by
323 vascular plants through the rhizosphere priming. The two-pool mixing model, taking into account
324 the CO_2 efflux and the corresponding ^{14}C signature in plots with and without vascular plants at
325 each peatland, shows a consistent enrichment of vascular plant-associated respiration with older
326 carbon, a result that clearly indicates a stimulation of heterotrophic peat decomposition through
327 the rhizosphere priming effect (Hardie *et al.*, 2009; Basiliko *et al.*, 2012; Walker *et al.*, 2016).
328 Although we cannot exclude a contribution of residual decomposing roots to the priming (even
329 after one year of decomposition), if this should take place in the clipped plots it means that the

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

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

342 On the basis of FT-IR spectroscopy, at both studied sites there was a higher humification
343 degree of dissolved organic matter in plots with intact vascular plants (Fig. 3), a result that seems
344 to reflect an enhanced microbial metabolism (Glatzel *et al.*, 2003; Höll *et al.*, 2009; Ward *et al.*,
345 2013; Lou *et al.*, 2014; Dieleman *et al.*, 2016). The removal of vascular plants is indeed expected
346 to reduce the availability of more labile, root-mediated carbon (Gogo *et al.*, 2011) that is used by
347 microbes for synthesising extracellular enzymes (Robroek *et al.*, 2016). Additionally, we observe
348 that warmer climatic conditions and larger vascular plant biomass are ultimately associated with a
349 larger release of dissolved organic carbon (DOC) in the peat soil at low elevation (Table 1). This
350 latter result points to the synergetic role of climate and vegetation in increasing the production
351 and release of DOC from peatlands (Neff & Hooper, 2002; Frey & Smith, 2005; Ward *et al.*,
352 2013; Kane *et al.*, 2014).

353 On the basis of the ^{14}C signature in the subsurface peat (Table 1), the estimated age of top 20
354 cm peat, particularly for the low elevation site, was in line with other studies (see e.g. Shotyk *et*
355 *al.*, 1997) suggesting a relatively recent peat accumulation, i.e. primarily after the bomb- ^{14}C peak
356 of 1963. We conclude that the carbon released by the priming effect was only a few decades old
357 (< 20 years) and stored above the mean water-table depth (Table 1). This observation highlights
358 the importance of water table in protecting peat from microbial decomposition (Ise *et al.*, 2008),
359 but also indicates the potential vulnerability of peat carbon if hydrological feedbacks to climate
360 change increase soil oxygenation (Waddington *et al.*, 2015) and, consequently, promote the
361 spreading of vascular plants (Dieleman *et al.*, 2015; Potvin *et al.*, 2015). The apparent rate of
362 carbon accumulation in the peat layers above the mean-water table depth approximated c. 90 g C
363 $\text{m}^{-2} \text{y}^{-1}$ for the low elevation site and c. $154 \text{ g C m}^{-2} \text{y}^{-1}$ for the high elevation site over a reference
364 period of 26-30 years for both sites, a result suggesting a lower carbon sink capacity of peatlands
365 at the lower end of their altitudinal distribution (Millar *et al.*, 2017). The effective annual
366 contribution of the rhizosphere priming to the observed difference in carbon accumulation rate in
367 relation to the dominant vascular plant functional types and their symbiotic microorganisms
368 remains an open question that deserves further attention (Gavazov *et al.*, 2016; Walker *et al.*,
369 2016; Sulman *et al.*, 2017).

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

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

382

383 **ACKNOWLEDGEMENTS**

384 We thank Lucas Wettstein and Adrian Pulgarin for field assistance and to Vincent Jassey and
385 Laurent Jeanneau for laboratory assistance. Thanks are also due to Ingeborg Levin and Samuel
386 Hammer for providing data on ¹⁴C signature of atmospheric CO₂. The Service des Forêts, de la
387 Faune et de la Nature (Canton de Vaud) and the Service de la promotion de la nature – Office de
388 l'agriculture et de la nature (Canton de Berne) are acknowledged for giving the permission to
389 access the studied peatlands. This work was supported by the Swiss National Science Foundation
390 grant number: 205320_144024 to L.B.

391

392 **REFERENCES**

- 393 Abramoff RZ, Finzi AC (2015) Are above- and below-ground phenology in sync? *New*
394 *Phytologist*, **205**, 1054–1061.
- 395 Armstrong A, Waldron S, Ostle NJ, Richardson H, Whitaker J (2015) Biotic and abiotic factors
396 interact to regulate northern peatland carbon cycling. *Ecosystems*, **18**, 1395–1409.
- 397 Bahn M, Schmitt M, Siegwolf R, Richter A, Brüggemann N (2009) Does photosynthesis affect
398 grassland soil-respired CO₂ and its carbon isotope composition on a diurnal timescale? *New*

- 399 *Phytologist*, **182**, 451–460.
- 400 Basiliko N, Stewart H, Roulet NT, Moore TR (2012) Do root exudates enhance eat
401 decomposition? *Geomicrobiology Journal*, **29**, 374–378.
- 402 Biester H, Knorr K-H, Schellekens J, Basler A, Hermanns Y-M (2014) Comparison of different
403 methods to determine the degree of peat decomposition in peat bogs. *Biogeosciences*, **11**,
404 2691–2707.
- 405 Blois JL, Williams JW, Fitzpatrick MC, Jackson ST, Ferrier S (2013) Space can substitute for
406 time in predicting climate-change effects on biodiversity. *Proceedings of the National
407 Academy of Sciences*, **110**, 9374–9379.
- 408 Blume-Werry G, Wilson SD, Kreyling J, Milbau A (2016) The hidden season: growing season is
409 50% longer below than above ground along an arctic elevation gradient. *New Phytologist*,
410 **209**, 978–986.
- 411 Bragazza L, Parisod J, Buttler A, Bardgett RD (2013) Biogeochemical plant-soil microbe
412 feedback in response to climate warming in peatlands. *Nature Climate Change*, **3**, 273–277.
- 413 Bragazza L, Buttler A, Robroek BJM, Albrecht R, Zaccone C, Jassey VEJ, Signarbieux C (2016)
414 Persistent high temperature and low precipitation reduce peat carbon accumulation. *Global
415 Change Biology*, **22**, 4114–4123.
- 416 Breeuwer A, Heijmans M, Robroek BJM, Berendse F (2010) Field Simulation of Global Change:
417 Transplanting Northern Bog Mesocosms Southward. *Ecosystems*, **13**, 712–726.
- 418 Broder T, Blodau C, Biester H, Knorr KH (2012) Peat decomposition records in three pristine
419 ombrotrophic bogs in southern Patagonia. *Biogeosciences*, **9**, 1479–1491.
- 420 Bubier J, Crill P, Mosedale A, Frohling S, Linder E (2003) Peatland responses to varying
421 interannual moisture conditions as measured by automatic CO₂ chambers. *Global*

- 422 *Biogeochemical Cycles*, **17**, no. 2, 1066.
- 423 Bubier JL, Moore TR, Bledzki LA (2007) Effects of nutrient addition on vegetation and carbon
424 cycling in an ombrotrophic bog. *Global Change Biology*, **13**, 1168–1186.
- 425 Chong M, Humphreys E, Moore TR (2012) Microclimatic response to increasing shrub cover and
426 its effect on *Sphagnum* CO₂ exchange in a bog. *Écoscience*, **19**, 89–97.
- 427 Conant RT, Ryan MG, Ågren GI et al. (2011) Temperature and soil organic matter
428 decomposition rates - synthesis of current knowledge and a way forward. *Global Change
429 Biology*, **17**, 3392–3404.
- 430 Czimczik CI, Trumbore SE, Carbone MS, Winston GC (2006) Changing sources of soil
431 respiration with time since fire in a boreal forest. *Global Change Biology*, **12**, 957–971.
- 432 Dieleman CM, Branfireun BA, McLaughlin JW, Lindo Z (2015) Climate change drives a shift in
433 peatland ecosystem plant community: Implications for ecosystem function and stability.
434 *Global Change Biology*, **21**, 388–395.
- 435 Dieleman CM, Lindo Z, McLaughlin JW, Craig AE, Branfireun BA (2016) Climate change
436 effects on peatland decomposition and porewater dissolved organic carbon biogeochemistry.
437 *Biogeochemistry*, **128**, 385–396.
- 438 Dorrepaal E (2007) Are plant growth-form-based classifications useful in predicting northern
439 ecosystem carbon cycling feedbacks to climate change? *Journal of Ecology*, **95**, 1167–1180.
- 440 Dorrepaal E, Toet S, van Logtestijn RSP, Swart E, van de Weg MJ, Callaghan T V., Aerts R
441 (2009) Carbon respiration from subsurface peat accelerated by climate warming in the
442 subarctic. *Nature*, **460**, 616–U79.
- 443 Fontaine S, Barot S, Barré P, Bdioui N, Mary B, Rumpel C (2007) Stability of organic carbon in
444 deep soil layers controlled by fresh carbon supply. *Nature*, **450**, 277–80.

- 445 Frey KE, Smith LC (2005) Amplified carbon release from vast West Siberian peatlands by 2100.
446 *Geophysical Research Letters*, **32**, L09401.
- 447 Garnett MH, Murray C (2013) Processing of CO₂ samples collected using zeolite molecular sieve
448 for ¹⁴C analysis at the NERC Radiocarbon Facility (East Kilbride, UK). *Radiocarbon*, **55**,
449 410–415.
- 450 Garnett MH, Hartley IP, Hopkins DW, Sommerkorn M, Wookey PA (2009) A passive sampling
451 method for radiocarbon analysis of soil respiration using molecular sieve. *Soil Biology and*
452 *Biochemistry*, **41**, 1450–1456.
- 453 Gavazov K, Hagedorn F, Buttler A, Siegwolf R, Bragazza L (2016) Environmental drivers of
454 carbon and nitrogen isotopic signatures in peatland vascular plants along an altitude
455 gradient. *Oecologia*, **180**, 257–264.
- 456 Glatzel S, Kalbitz K, Dalva M, Moore T (2003) Dissolved organic matter properties and their
457 relationship to carbon dioxide efflux from restored peat bogs. *Geoderma*, **113**, 397–411.
- 458 Gogo S, Laggoun-Défarge F, Delarue F, Lottier N (2011) Invasion of a Sphagnum-peatland by
459 *Betula* spp and *Molinia caerulea* impacts organic matter biochemistry. Implications for
460 carbon and nutrient cycling. *Biogeochemistry*, **106**, 53–69.
- 461 Goodsite ME, Rom W, Heinemeier J et al. (2001) High-resolution AMS ¹⁴C dating of post-bomb
462 peat archives of atmospheric pollutants. *Radiocarbon*, **43**, 495–515.
- 463 Hájek T, Ballance S, Limpens J, Zijlstra M, Verhoeven JTA (2011) Cell-wall polysaccharides
464 play an important role in decay resistance of *Sphagnum* and actively depressed
465 decomposition in vitro. *Biogeochemistry*, **103**, 45–57.
- 466 Hardie SML, Garnett MMH, Fallik AE et al. (2007) Spatial variability of bomb ¹⁴C in an upland
467 peat bog. *Radiocarbon*, **49**, 1055–1063.

- 468 Hardie SML, Garnett MH, Fallick AE, Ostle NJ, Rowland AP (2009) Bomb-¹⁴C analysis of
469 ecosystem respiration reveals that peatland vegetation facilitates release of old carbon.
470 *Geoderma*, **153**, 393–401.
- 471 Hartley IP, Garnett MH, Sommerkorn M et al. (2012) A potential loss of carbon associated with
472 greater plant growth in the European Arctic. *Nature Climate Change*, **2**, 875–879.
- 473 Hicks Pries CE, Schuur EAG, Crummer KG (2013) Thawing permafrost increases old soil and
474 autotrophic respiration in tundra: Partitioning ecosystem respiration using $\delta^{13}\text{C}$ and $\Delta^{14}\text{C}$.
475 *Global Change Biology*, **19**, 649–661.
- 476 Hicks Pries CE, van Logtestijn RSP, Schuur EAG, Natali SM, Cornelissen JHC, Aerts R,
477 Dorrepaal E (2015) Decadal warming causes a consistent and persistent shift from
478 heterotrophic to autotrophic respiration in contrasting permafrost ecosystems. *Global*
479 *Change Biology*, **21**, 4508–4519.
- 480 Hirano T, Yamada H, Takada M, Fujimura Y, Fujita H, Takahashi H (2016) Effects of the
481 expansion of vascular plants in *Sphagnum*-dominated bog on evapotranspiration.
482 *Agricultural and Forest Meteorology*, **220**, 90–100.
- 483 Hodgkins SB, Tfaily MM, McCalley CK et al. (2014) Changes in peat chemistry associated with
484 permafrost thaw increase greenhouse gas production. *Proceedings of the National Academy*
485 *of Sciences*, **111**, 5819–5824.
- 486 Höll BS, Fiedler S, Jungkunst HF, Kalbitz K, Freibauer A, Drösler M, Stahr K (2009)
487 Characteristics of dissolved organic matter following 20 years of peatland restoration.
488 *Science of The Total Environment*, **408**, 78–83.
- 489 Ise T, Dunn AL, Wofsy SC, Moorcroft PR (2008) High sensitivity of peat decomposition to
490 climate change through water-table feedback. *Nature Geoscience*, **1**, 763–766.

- 491 Juutinen S, Bubier JL, Moore TR (2010) Responses of vegetation and ecosystem CO₂ exchange
492 to 9 years of nutrient addition at Mer Bleue bog. *Ecosystems*, **13**, 874–887.
- 493 Kane ES, Mazzoleni LR, Kratz CJ, Hribljan JA, Johnson CP, Pypker TG, Chimner R (2014) Peat
494 porewater dissolved organic carbon concentration and lability increase with warming: A
495 field temperature manipulation experiment in a poor-fen. *Biogeochemistry*, **119**, 161–178.
- 496 Klaus G (2007) *État et évolution des marais en Suisse. Résultats du suivi de la protection des*
497 *marais. Etat de l'environnement no 0730*. Office fédéral de l'environnement, Berne,
498 Switzerland, 97 pp.
- 499 Kuiper JJ, Mooij WM, Bragazza L, Robroek BJM (2014) Plant functional types define magnitude
500 of drought response in peatland CO₂ exchange. *Ecology*, **95**, 123–131.
- 501 Kuzyakov Y (2010) Priming effects: Interactions between living and dead organic matter. *Soil*
502 *Biology and Biochemistry*, **42**, 1363–1371.
- 503 Laiho R, Laine J, Trettin CC, Finér L (2004) Scots pine litter decomposition along drainage
504 succession and soil nutrient gradients in peatland forests, and the effects of inter-annual
505 weather variation. *Soil Biology and Biochemistry*, **36**, 1095–1109.
- 506 Laine AM, Bubier JL, Riutta T, Nilsson MB, Moore TR, Vasander H, Tuittila E-S (2012)
507 Abundance and composition of plant biomass as potential controls for mire net ecosystem
508 CO₂ exchange. *Botany*, **90**, 63–74.
- 509 Leppälä M, Kukko-Oja K, Laine J, Tuittila E-S (2008) Seasonal dynamics of CO₂ exchange
510 during primary succession of boreal mires as controlled by phenology of plants. *Écoscience*,
511 **15**, 460–471.
- 512 Levin I, Hammer S, Kromer B, Meinhardt F (2008) Radiocarbon observations in atmospheric
513 CO₂: Determining fossil fuel CO₂ over Europe using Jungfrauoch observations as

- 514 background. *Science of the Total Environment*, **391**, 211–216.
- 515 Levin I, Kromer B, Hammer S (2013) Atmospheric $\Delta^{14}\text{CO}_2$ trend in Western European
516 background air from 2000 to 2012. *Tellus B: Chemical and Physical Meteorology*, **65**.
- 517 Lou XD, Zhai SQ, Kang B, Hu YL, Hu LL (2014) Rapid response of hydrological loss of DOC
518 to water table drawdown and warming in Zoige peatland: Results from a mesocosm
519 experiment. *PLoS ONE*, **9**, 19–21.
- 520 Luo Z, Wang E, Sun OJ (2016) A meta-analysis of the temporal dynamics of priming soil carbon
521 decomposition by fresh carbon inputs across ecosystems. *Soil Biology Biochemistry*, **10**, 96-
522 103.
- 523 Millar DJ, Cooper DJ, Dwire KA, Hubbard RM, von Fischer J (2017) Mountain peatlands range
524 from CO_2 sinks at high elevations to sources at low elevations: Implications for a changing
525 climate. *Ecosystems*, **20**, 416–432.
- 526 Moore TR, Bubier JL, Bledzki L (2007) Litter decomposition in temperate peatland ecosystems:
527 The effect of substrate and site. *Ecosystems*, **10**, 949–963.
- 528 Munir TM, Perkins M, Kaing E, Strack M (2015) Carbon dioxide flux and net primary
529 production of a boreal treed bog: Responses to warming and water-table-lowering
530 simulations of climate change. *Biogeosciences*, **12**, 1091–1111.
- 531 Murphy MT, McKinley A, Moore TR (2009) Variations in above- and below-ground vascular
532 plant biomass and water table on a temperate ombrotrophic peatland. *Botany*, **87**, 845–853.
- 533 Natali SM, Schuur EAG, Trucco C, Hicks Pries CE, Crummer KG, Baron Lopez AF (2011)
534 Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan
535 tundra. *Global Change Biology*, **17**, 1394–1407.
- 536 Neff JC, Hooper DU (2002) Vegetation and climate controls on potential CO_2 , DOC and DON

- 537 production in northern latitude soils. *Global Change Biology*, **8**, 872–884.
- 538 Niemeyer J, Chen Y, Bollag J (1992) Characterization of humic acids, composts, and peat by
539 diffuse reflectance fourier-transform infrared-spectroscopy. *Soil Science Society of America*
540 *Journal*, **56**, 135–140.
- 541 Philben M, Kaiser K, Benner R (2014) Does oxygen exposure time control the extent of organic
542 matter decomposition in peatlands? *Journal of Geophysical Research: Biogeosciences*, **119**,
543 897–909.
- 544 Piao S, Ciais P, Friedlingstein P et al. (2008) Net carbon dioxide losses of northern ecosystems in
545 response to autumn warming. *Nature*, **451**, 49–52.
- 546 Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2016) nlme: Linear and Nonlinear
547 Mixed Effects Models. R package version 3.1-128.
- 548 Potvin LR, Kane ES, Chimner RA, Kolka RK, Lilleskov EA (2015) Effects of water table
549 position and plant functional group on plant community, aboveground production, and peat
550 properties in a peatland mesocosm experiment (PEATcosm). *Plant and Soil*, **387**, 277–294.
- 551 Qiao N, Schaefer D, Blagodatskaya E, Zou X, Xu X, Kuzyakov Y (2014) Labile carbon retention
552 compensates for CO₂ released by priming in forest soils. *Global Change Biology*, **20**, 1943–
553 1954.
- 554 R Core Team (2016) R: A language and environment for statistical computing.
- 555 Reimer PJ, Brown, TA, and Reimer, RW (2004) Discussion: Reporting and calibration of post-
556 bomb 14C data. *Radiocarbon*, **46**, 1299-1304.
- 557 Robroek BJM, Albrecht RJH, Hamard S, Pulgarin A, Bragazza L, Buttler A, Jassey VE (2016)
558 Peatland vascular plant functional types affect dissolved organic matter chemistry. *Plant and*
559 *Soil*, **407**, 135–143.

- 560 Schmidt MWI, Torn MS, Abiven S et al. (2011) Persistence of soil organic matter as an
561 ecosystem property. *Nature*, **478**, 49–56.
- 562 Shotykh W, Cheburkin AK, Appleby PG, Fankhauser A, Kramers JD (1997) Lead in three peat
563 bog profiles, Jura Mountains, Switzerland: enrichment factors, isotopic composition, and
564 chronology of atmospheric deposition. *Water Air and Soil Pollution*, **100**, 297–310.
- 565 Singh S, Inamdar S, Mitchell M, McHale P (2014) Seasonal pattern of dissolved organic matter
566 (DOM) in watershed sources: Influence of hydrologic flow paths and autumn leaf fall.
567 *Biogeochemistry*, **118**, 321–337.
- 568 Stuiver M, Polach HA (1977) Reporting of ^{14}C data. Discussion. *Radiocarbon*, **19**, 355–363.
- 569 Subke JA, Voke NR, Leronni V, Garnett MH, Ineson P (2011) Dynamics and pathways of
570 autotrophic and heterotrophic soil CO_2 efflux revealed by forest girdling. *Journal of*
571 *Ecology*, **99**, 186–193.
- 572 Sulman BN, Brzostek ER, Medici C, Shevliakova E, Menge DNL, Phillips RP (2017) Feedbacks
573 between plant N demand and rhizosphere priming depend on type of mycorrhizal
574 association. *Ecology Letters*, **20**, 1043–1053.
- 575 Talbot J, Roulet NT, Sonnentag O, Moore TR (2014) Increases in aboveground biomass and leaf
576 area 85 years after drainage in a bog. *Botany*, **92**, 713–721.
- 577 Updegraff K, Bridgman SD, Pastor J, Weishampel P, Harth C (2001) Response of CO_2 and CH_4
578 emissions from peatlands to warming and water table manipulation. *Ecological*
579 *Applications*, **11**, 311–326.
- 580 Waddington JM, Morris PJ, Kettridge N, Granath G, Thompson DK, Moore PA (2015)
581 Hydrological feedbacks in northern peatlands. *Ecohydrology*, **8**, 113–127.
- 582 Walker TN, Garnett MH, Ward SE, Oakley S, Bardgett RD, Ostle NJ (2016) Vascular plants

- 583 promote ancient peatland carbon loss with climate warming. *Global Change Biology*, **22**,
584 1880–1889.
- 585 Wang H, Richardson CJ, Ho M (2015) Dual controls on carbon loss during drought in peatlands.
586 *Nature Climate Change*, **5**, 584–588.
- 587 Ward SE, Bardgett RD, McNamara NP, Ostle NJ (2009) Plant functional group identity
588 influences short-term peatland ecosystem carbon flux: Evidence from a plant removal
589 experiment. *Functional Ecology*, **23**, 454–462.
- 590 Ward SE, Ostle NJ, Oakley S, Quirk H, Henrys PA, Bardgett RD (2013) Warming effects on
591 greenhouse gas fluxes in peatlands are modulated by vegetation composition. *Ecology*
592 *Letters*, **16**, 1285–1293.
- 593 Weltzin JF, Pastor J, Harth C, Bridgham SD, Updegraff K, Chapin CT (2000) Response of bog
594 and fen plant communities to warming and water table manipulations. *Ecology*, **81**, 3464–
595 3478.
- 596 Yu ZC (2012) Northern peatland carbon stocks and dynamics: A review. *Biogeosciences*, **9**,
597 4071–4085.
- 598 Zhu B, Cheng W (2011) Rhizosphere priming effect increases the temperature sensitivity of soil
599 organic matter decomposition. *Global Change Biology*, **17**, 2172–2183.
- 600

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 ($\mu\text{S cm}^{-1}$)	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 σ)	16 / 110.23 \pm 0.48	1 / 103.41 \pm 0.47
Age at 10-15 cm (years / %Mod ¹⁴ C \pm 1 σ)	30 / 120.75 \pm 0.53	16 / 110.01 \pm 0.48
Age at 15-20 cm (years / %Mod ¹⁴ C \pm 1 σ)	40 / 139.28 \pm 0.61	26 / 117.12 \pm 0.51

FIGURE CAPTIONS

Fig. 1 Seasonal dynamics of ecosystem CO₂ 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 CO₂ 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 CO₂.

Fig. 2 ¹⁴C content of ecosystem respired CO₂ 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 ¹⁴C-CO₂ associated with the presence of vascular plants (DV_plant_associated). Dotted line indicates the mean atmospheric ¹⁴C-CO₂ 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.





